Univerzita Karlova

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# Dizertační práce

## Interakce rostlin a hmyzu ve spodním miocénu střední Evropy v paleoklimatologických a paleoekologických souvislostech

## Plant – insect interactions in lower Miocene of Central Europe: palaeoclimatological and palaeoecological implications

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# Abstrakt

Paleoekologie vzájemných vztahů členovců a rostlin a jejich trofických asociací představuje velmi významný zdroj znalostí o fylogenezi a koevoluci obou skupin. Fosilní stopy herbivorie členovců na fosilních listech jsou zachovány ve formě tzv. typů poškození (Damage Types), seskupených do odlišných funkčně potravních skupin (FFGs). Rozmanitost a četnost tohoto typu interakcí byly v minulosti výrazně ovlivněny okolními environmentálními a klimatickými podmínkami. Tato studie byla zaměřena na bohaté paleobotanické soubory z oblasti mostecké pánve v severozápadních Čechách. Výzkum zahrnoval diagnózu jednotlivých typů poškození na základě jejich specifických morfologických znaků, počtu, velikosti, tvaru a rozmístění na povrchu listů. Poté následovalo statistické zpracování, které se zaměřilo zejména na rozdíly v četnosti a rozmanitosti typů poškození a funkčně potravních skupin mezi dvěma na sebe navazujícími fosiliferními celky, jmenovitě staršími uloženinami bílinské delty a stratigraficky mladšími břešťanskými jíly. V tomto směru byly potvrzené významné rozdíly, které se týkaly zejména vyšší četnosti a proporcionálního výskytu odlišných funkčně potravních skupin dosažených v souboru bílinské delty. Jedinou výjimkou byla tvorba hálek, která dosahovala v souboru břešťanských jílů až čtyřnásobně vyšší hodnoty oproti uloženinám bílinské delty. Tato zjištění nasvědčují spíše teplejším klimatickým podmínkám v prostředí bílinské delty a zjevně suššímu prostředí břešťanských jílů.

Sledované jednotlivé rostlinné taxony vykazují rovněž značné rozdíly v četnosti různých funkčně potravních skupin a diverzně odlišných typů poškození. Mezi jednotlivými funkčně potravními skupinami převažuje dutinový žír, následován okrajovým žírem a tvorbou hálek. Nejvíce zasaženými různými typy žírů se jeví být tenkolisté opadavé dřeviny, zvláště druhy *Carya* sp a *Populus zaddachii*. Tento typ dřevin, mezi něž patří i rody, *Acer, Alnus, Fraxinus, Nyssa* a *Populus* také dosahují nejvyšší rozmanitosti odlišných typů poškození. Na druhou stranu, stálezelený dub druhu *Quercus rhenana* se svými kožovitými listy vykazuje rovněž poměrně velkou rozmanitost poškození. Zbývající taxony až na několik výjimek pak dosahují spíše vyrovnaných hodnot diverzity v rámci odlišných typů poškození. Porovnání závislosti dosažené diverzity všech typů poškození na četnosti jejich výskytu v rámci početně dostatečně zastoupených rostlinných taxonů poškození prokazuje mírně pozitivní korelaci, podobně jako je tomu v případě hálek.

V některých zvláště vhodných případech specifických interakcí bylo možné dosáhnout detailního taxonomického určení původců, což usnadňuje vhledem ke známým ekologickým nárokům jejich recentních příbuzných stanovení tehdejších environmentálních podmínek. Mezi ty nejdůležitější náleží zejména různí původci hálek z čeledí Cynipidae (Hymenoptera) a Cecidomyiidae (Diptera), dále minující larva nočního motýla z čeledi Nepticulidae (Lepidoptera). Diagniostikována byla rovněž ovipozice šidélka (Odonata: Lestidae) a otisky schránek červců (Hemiptera: Coccoidea). Zajímavý je rovněž nález schránek chrostíků, popřípadě motýlů z čeledi Psychidae (Lepidoptera) zbudované výlučně z taxodiových jehlic. Mezi další zajímavé vzorky patří například výskyt apothécií hub (Pyrenomycetes) na zkamenělé kůře povrchu a dalších, dosud neidentifikovaných hub na povrchu listů, indikujících rozkladné procesy.

# Abstract

The paleoecology of plant – arthropod herbivory associations constitute very important source of knowledge about the phylogeny and co-evolution of both groups. The traces of herbivory interactions between plants and arthropods on the fossil leaves are preserved as so called damaged types (DTs) clustered into distinct functional feeding groups (FFGs). The diversity and frequency of these damage traces also seem to have been strongly influenced by environmental and climatic conditions. This research has been focused on rich fossil plant assemblages from the area of the Most Basin in the north-western Bohemia. The undergoing work has comprised the diagnosis of the individual damages on the basis of their specific morphological traits as their number, size, shape and distributional pattern on the leaf surface. The next issue has involved the statistical analyses concerning the differences in the frequency and diversity of the types of damage and functional feeding groups between two separate fossiliferous layers, namely those of the stratigraphically older Bílina Delta and younger Břešťany Clay. Significant differences were confirmed in this regard, especially in connection with achieved frequency and proportional occurrences of distinct functional feeding groups in the Bílina Delta. The galls were the only exception, being much more frequent in Břešťany Clay. The obtained differences concerning the damage diversity were less significant. These circumstances indicate possibly a little bit warmer climatic condition in the Bílina Delta, but certainly the drier one in Břešťany Clay.

The observed individual taxa also show significant differences in frequencies of various functional feeding groups and the diversity of the distinct damage types. Among individual functional feeding groups, those of hole feeding, followed by margin feeding and galling are the most common. Arboreal deciduous elements, such as *Populus zaddachii* and *Carya* sp., seem to be the most affected. Taxa with chartaceous leaf texture (*Acer*, *Alnus*, *Fraxinus*, *Nyssa* and *Populus*) also attain the highest diversity of distinct damage types. On the other hand, *Quercus rhenana*, with its coriaceous texture of foliage, shows also fairly high diversity of damage. Otherwise, the comparison of the DT diversity among these individual taxa provides rather uniform outputs. There is no substantial difference with the exception of the few taxa with extreme values. Comparing how the diversity of DTs depends on DT frequency confirms a slight increase in tendency, although this correlation appears to be very weak. Corresponding results are also recorded for the different types of arthropod galls.

Taxonomic attribution of some possible causers has been also made in especially suitable cases, allowing the setting of a certain palaeoenvironmental conditions due to their known ecological requirements. The most important findings are represented by various cynipid wasps (Hymenoptera) and cecidomyid flies (Diptera) galls, nepticulid moths (Lepidoptera) leaf mine, odonatan (probably Lestidae) oviposition on the willow leaf and a spectacular impression of the scale insect (Hemiptera: Coccoidea) on the leaf of ash. One remarkable non-herbivore plant-arthropod interaction was newly characterized by several records of caddisfly cases (immature stage of the family Psychidae (Lepidoptera) can be the alternative explanation) built exclusively of needles of *Taxodium*. The other interesting specimens show for instance the presence of fungal apothecia (Pyrenomycetes) on the fossilized bark surface and the other ones on the unidentified leaf surface, indicating progressive decaying processes.

# Obsah

# 1 Úvod do problematiky

## 1.1 Stopy interakcí rostlin a členovců ve fosilním záznamu

Hned na počátku je třeba konstatovat, že ač v názvu této práce zaznívá explicitně slovo hmyz, do výzkumu jsou zahrnuty i projevy působení ostatních členovců (Arthropoda), zejména pak roztočů (Acari). Samotné počátky vzájemného působení hmyzu resp. členovců a rostlin se datují hluboko do minulosti. Nejstarší doklady pravděpodobně hmyzího žíru, popsaného na listech kapraďosemenné rostliny druhu *Triphyllopteris austrina*, sice pocházejí až z konce spodního karbonu Austrálie (Iannuzzi a Labandeira, 2008), původ členovčí herbivorie je však nepochybně ještě mnohem staršího data. Pro tuto skutečnost svědčí kupříkladu nálezy povrchové abraze peridermálních a epidermálních pletiv na fotosyntetizujících stoncích dvou různých zástupců bezlistého rodu Psilophyton z oddělení Trimerophytophyta z kanadského spodního devonu (Banks a Colthart, 1993, Trant a Gensel, 1985). Obě poškození vykazují stopy regenerativní proliferace okolního pletiva včetně tvorby závalu, což jednoznačně hovoří pro konzumaci vitální rostliny. Obdobného stáří je i nejstarší dochovaný list náležející druhu *Eophyllophyton bellum* ze skupiny Progymnosperma, pocházející ze spodního devonu (stupeň prag) provincie Junnan v Číně (Hao a Beck, 1993). To mimo jiné dokazuje, že již v období nástupu prvních makrofylních rostlin existovala herbivorní mikroarthropoda s dostatečně účinným mandibulátním typem ústního ústrojí. Jako nejstarší doklad existence ektognátního hmyzu (Insecta *sensu stricto*) je pak interpretován fragmentární nález ústního ústrojí rovněž ze spodnodevonských uloženin, tentokráte však skotské lokality Rhynie Chert, který byl popsán jako *Rhyniognatha hirsti* HIRST et MAULIK, 1926 (Hirst a Maulik, 1926). Z této lokality jsou známy též koprolity obsahující zbytky různých rostlinných pletiv a spor (Habgood a kol., 2004). Nicméně, až do svrchního karbonu se podobně nálezy, zejména ty dokládající folivorii, vyskytují jen vzácně. Přibývat jich začíná až zhruba od druhé poloviny této epochy, kdy jsou zdokumentovány hlavně z tehdejší euroamerické rovníkové oblasti (Scott a Taylor, 1983; Scott a kol., 1992; Labandeira, 1998a).

Počínaje touto dobou se mezi členovci a rostlinami začala postupně vytvářet velmi komplikovaná a delikátní síť nejen trofických vazeb, které v průběhu evoluce zásadním způsobem, ať již přímo či nepřímo ovlivnily a nadále ovlivňují většinu ostatních terestrických organismů včetně člověka. Ty, které zanechaly svou stopu ve fosilním záznamu, nabízejí možnost hlubšího pochopení proměn těchto evolučních vztahů v čase. Některé jiné naopak dokládají jejich pozoruhodnou starobylost a stálost. Kvalitativní a kvantitativní analýza

vybraných typů interakcí vykazujících vyšší citlivost ke změnám prostředí zase přispívá k poznání dynamiky dávno zaniklých ekosystémů a klimatických změn v geologické minulosti. Stopy členovčí herbivorie jakož i ovipozice popřípadě stavby různých schránek jsou podobně jako stopy činnosti ostatních organismů ve fosilním substrátu řazeny k ichnofosiliím, které je často zvykem klasifikovat jako samostatné ichnotaxony (Mikuláš a kol., 2003; Sarzetti a kol., 2009).

Současný výzkum dochovaných interakcí se v zásadě ubírá dvěma různými, byť částečně se překrývajícími směry. V prvním případě se jedná o detailní studium jejich evolučně-morfologických aspektů, umožňujících poté komplexní systematické i paleobiogegrafické interpretace příslušných nálezů. V tom druhém stojí v popředí výzkum z hlediska paleoekologicko – paleoklimatologického, mapující dynamiku diverzity herbivorie a relativní četnosti jednotlivých funkčně potravních skupin i typů poškození v závislosti na změnách klimatu a prostředí. Oba tyto přístupy se vzájemně doplňují a představují tak jeden z relativně komplexních zdrojů poznatků o vývoji globálního ekosystému v minulosti.

### 1.1.1 Interakce jako doklad koevoluce členovců a rostlin

Toto pojetí výzkumu interakcí se opírá především o podrobné studium morfologických charakteristik jejich jednotlivých typů interakcí a je proto závislé na velmi dobrém stupni zachování zkoumaných nálezů. Pokud jde o nejrůznější případy okusů, většina z nich není příliš rodově nebo dokonce druhově specifických. Jednu z mála výjimek představuje nezaměnitelný typ vnějšího okusu v podobě specifického výkrojku způsobeného zástupci čeledi Megachilidae (Hymenoptera) na listech z eocenní lokality Messel (Wappler a Engel, 2003; Wedmann a kol., 2009). Do popředí vědeckého zájmu se proto dostávají zejména morfologicky unikátní typy interakcí, jako jsou tvorba hálek (*galling*) a minující žír (*mining*), které dávají dobrou možnost taxonomické determinace svých původců na základě srovnávacích studií s druhy recentními (Hickey a Hodges, 1975; Opler, 1982; Erwin a Schick, 2007; Wappler a Ben-Dov, 2008). Dalším, díky svým charakteristickým rysům rovněž dobře diagnostikovatelným typem interakce, je ovipozice (Sarzetti a kol., 2009; Petrulevičius a kol., 2011; Laaß a Hoff, 2014). Nicméně ač se ve všech výše uvedených případech jedná o asociace velmi konzervativní, jejich taxonomického určení, alespoň pokud jde o stupeň příbuznosti s recentními zástupci, je obvykle proveditelné jen do úrovně čeledi, popřípadě rodu. Každopádně je to právě co nejpřesnější taxonomické určení, které představuje jednu ze základních podmínek všech případných fylogeneticko – paleobiogeografických implikací. Vzhledem ke známému biogeografickému rozšíření a ekologickým nárokům dnes žijících

zástupců těchto čeledí a rodů lze využít tyto poznatky k lepšímu porozumění zákonitostí jejich původu, vývoje a současného rozšíření. V tomto ohledu se jeví jako nejperspektivnější nálezy z paleogénu a neogénu, které již jeví velkou morfologickou podobnost s jejich recentními protějšky (Hickey a Hodges, 1975; Opler, 1973; 1982; Wappler a Engel, 2003; Erwin a Schick, 2007; Wedmann a kol., 2009).

### 1.1.2 Interakce jako paleoenvironmentální a paleoklimatická proxy

Tento způsob využití interakcí členovců a rostlin ve fosilním záznamu představuje frekventovanější z obou výzkumných přístupů. Jak již bylo uvedeno, soustředí se na celkové zhodnocení rozložení jejich četnosti a diverzity v čase a prostoru. Porovnáním těchto kvantitativních charakteristik mezi jednotlivými lokalitami různého stáří lze do určité míry vysledovat změny tehdejších klimatických podmínek (např. Wilf a Labandeira, 1999; Labandeira a kol., 2002; Wilf a kol., 2001; Wappler, 2010; Wappler a kol. 2012; Gunkel a Wappler, 2015). Popřípadě je výsledky takovéhoto výzkumu možné začlenit do širšího paleoenvironmentálního kontextu a přispět tak k objasnění kauzality příslušných změn dynamiky vzájemných vztahů mezi hmyzem a jeho rostlinnými hostiteli v důsledku nejrůznějších globálních eventů (např. Labandeira a kol., 2002; Wilf a Johnson, 2004; Wilf a kol., 2006; Wappler a kol., 2009; Donovan a kol., 2014). Výzkumy, které se zpočátku soustředily na evropské a severoamerické lokality, se postupně rozšiřují i na další světové oblasti, a získané informace je tak možné porovnávat v rámci odlišných zeměpisných pásem a biogeografických oblastí (Wilf a kol., 2005; Wappler a Denk, 2011; Khan a kol., 2014; McLoughlin a kol., 2015). Další studie se zaměřují na diagnostiku nejrůznějších typů poškození ve snaze o rozlišení jednotlivých původců nejen z řad členovců, ale i nematod, hub, bakterií a virů a dosažení hlubšího porozumění koevoluce všech těchto zúčastněných skupin organismů a jejich vzájemného působení (Labandeira a Prevec, 2014). Výše uvedené studie přitom vycházejí z níže uvedených teoretických předpokladů, které jsou velmi dobře shrnuty v řadě souhrnných pojednání (např. Labandeira, 1998b; Wilf, 2008).

Na základě empirických zjištění lze stanovit tři základní bioklimatické faktory zásadním způsobem ovlivňující četnost a diverzitu různých typů poškození způsobených herbivorní aktivitou hmyzu a ostatních členovců (Wilf, 2008). V prvé řadě se jedná o teplotu prostředí. Je známým faktem, že směrem k rovníku stoupá biodiverzita a tedy i rozmanitost hmyzí fauny. Proto nepřekvapuje, že v souvislosti s tímto jevem dochází i přes nejrůznější obranné mechanismy hostitelských rostlin rovněž k nárůstu rozmanitosti nejrůznějších typů herbivorních asociací (Coley a Aide, 1991; Coley a Barone, 1996). Pokud jde o zvyšující se

rozsah a četnost poškození rovněž se úměrně zvyšující v relaci k okolní teplotě, oba tyto jevy mohou být zapříčiněny vyšším stupněm metabolismu a z toho vyplývajících aktivit, jako jsou příjem potravy a rozmnožování (Brown a kol., 2004, Allen a kol., 2006). Alternativním vysvětlením, alespoň co se týče kolísání intenzity hmyzí herbivorie v minulosti, mohou být změny $pCO_2$ v atmosféře. Zvýšený obsah a tedy parciální tlak tohoto skleníkového plynu je totiž jedním z faktorů (zdaleka však ne jediným a zřejmě ani nejdůležitějším) ovlivňujícím globální teplotní poměry. Podle této teorie vyšší podíl $CO_2$ v atmosféře zapříčiňuje nižší obsah dusíku v rostlinných pletivech, což indukuje nutnost jejich zvýšené konzumace hmyzími herbivory. Experimentální potvrzení tohoto tvrzení je však přinejmenším sporné (Zvereva a Kozlov, 2006; Adler a kol., 2007). Navíc samozřejmě nedává odpověď na příčinu vzrůstající intenzity herbivorie v závislosti na snižující se zeměpisné šířce v recentních ekosystémech, kde je hladina $pCO_2$ srovnatelná. Každopádně v průběhu minulosti lze vysledovat značné kolísání této veličiny, kupříkladu na základě studia hustoty průduchů na fosilních listech (Royer, 2001; Kürschner a kol., 2008). Nicméně, četné paleobiologické studie opravdu dokládají zvyšující se diverzitu i četnost výskytu herbivorních asociací v souvislosti s nárůstem lokálních teplot. Existuje totiž řada metod (viz níže), jak odvodit teplotní parametry charakterizující příslušné prostředí v minulosti, které pak slouží jako poměrně spolehlivé vodítko k uvedeným závěrům. Jako příklad lze uvést řadu studií zabývajících se rostlinnými společenstvy z rozdílných geologických vrstev v rámci jedné či více lokalit a jejich vzájemným porovnáním i z hlediska hmyzích interakcí (Wilf a Labandeira, 1999; Wilf a kol., 2006; Currano a kol., 2008).

Dalším významným faktorem, majícím vliv na četnost a diverzitu herbivorních asociací rostlin a hmyzu, je množství atmosférických srážek. Děje se tak ovšem nepřímo, prostřednictvím působením tohoto faktoru na fyziologii a anatomii rostlin, zvláště pak jejich listoví. Malé množství srážek, popřípadě jejich značně nerovnoměrný přísun projevující se dlouhými údobími sucha, selektují u rostlin četné morfologické adaptace, zahrnující také minimalizaci jejich plochy ve vztahu k jejich celkovému objemu. Listy jsou tak menší a mají větší tloušťku (Givnish, 1987). Tento vztah lze popsat pomocí veličiny $M_A$, tedy hmotnosti listu na jednotku jeho plochy (*Leaf mass per area*). Ta nabývá vyšších hodnot v závislosti na zvyšujícím se deficitu tlaku vodních par (*Vapor pressure deficit*, VPD) a potenciální úrovní transpirace zejména u stálezelených dřevin, nikoli však u opadavých (Wright a kol., 2005). Naopak, obsah dusíku (*Mass-based N*) za daných okolností klesá a tím pádem i nutriční hodnota listového pletiva. Listy xerofilních a stálezelených rostlin v důsledku toho disponují menšími, silnějšími a zpravidla také tužšími, méně výživnými listy, navíc s delší životností a

lepší mechanickou i chemickou ochranou proti herbivorům (nejen proti těm hmyzím, jejich stonky a kmeny jsou často vybaveny rovněž trny). Všechny jmenované faktory (snad až na deficit dusíku; ten by měl intenzitu herbivorie spíše zvyšovat, neboť herbivoři jich musí zkonzumovat více) přispívají k nižší úrovni herbivorie v ekosystému (Coley, 1983; Basset, 1994; Poorter a kol., 2004; Royer a kol., 2007). Royer a kol. (2007) vyvinuli metody měření $M_A$ i na fosilních listech a prokázali platnost výše uvedených zjištění i na příkladu dvou severoamerických paleobotanických lokalit. Pozoruhodnou výjimku představuje v této souvislosti tvorba hálek, která vykazuje v sušším klimatu naopak vzestupnou tendenci jak co do diverzity, tak co do četnosti jednotlivých afekcí (Fernandes and Price, 1988, 1991; Wright and Samways, 1998). Největší intenzity dosahuje tvorba hálek v oblastech sklerofylní vegetace mediteránního typu, níže směrem k rovníku tohoto pozoruhodného typu asociace vlivem vysoké atmosférické vlhkosti ubývá, neboť tato zvyšuje zranitelnost jeho původců ze strany různých parazitoidů a patogenů, zejména plísní (Godfray, 1994; Price a kol., 1998; Cuevas-Reyes a kol., 2004).

A nakonec jako poslední, nicméně možná nejdůležitější faktor ovlivňující všechny pozorované kvantitativní parametry herbivorních interakcí, lze uvést celkovou diverzitu hostitelských rostlin. Toto tvrzení podporuje většina autorů, zabývajících se touto problematikou (Wright a Samways, 1998; Knops a kol., 1999; Hawkins a Porter, 2003; Dyer a kol., 2007). Vzhledem k tomu, že většina hmyzích herbivorů je značně specializovaná a tudíž závislá na omezeném okruhu hostitelů rostliny (Bernays a Chapman, 1994; Schoonhoven a kol., 2005), jsou jednotlivé druhy poměrně zranitelné v důsledku jejich náhlého vymizení. Paleontologické studie na toto téma se většinou soustředí na období rozsáhlých vymírání na konci permu a křídy, kdy došlo k rozsáhlé destrukci stávajících ekosystémů. Výstupy těchto výzkumů nepřekvapivě potvrzují propad diverzity i frekvence herbivorie hmyzu i dalších členovců v závislosti na ochuzení spektra rostlinných druhů (Labandeira a kol., 2002; Wilf a kol., 2003; Wilf a Johnson, 2004; Currano a kol., 2008).

### 1.1.3 Rostlinná společenstva jako paleoklimatická proxy

Pomineme-li fyzikální metody zkoumající obsah stabilních izotopů prvků ($\delta^2H$, $\delta^{18}O$, $\delta^{13}C$), popřípadě jejich poměry (Sr/Ca, Mg/Ca) v různých substrátech, v souvislosti s výzkumem interakcí mají asi největší význam proxy data získaná rozborem vybraných charakteristik příslušné lokální paleoflóry. V současné době existují dva okruhy přístupů jak využít fosilní rostlinná společenstva ke stanovení místních klimatických poměrů. První a jednodušší je ten založený na posouzení taxonomické příbuznosti příslušných rostlinných

druhů s druhy recentními. Vychází z předpokladu velmi podobných klimatických a ekologické nároků jaké má nejbližší žijící druh (*Nearest living relative*, NRL – MacGinitie, 1941; Chaloner a Creber, 1990; Mosbrugger, 1999). Průkaznost tohoto přístupu je někdy diskutována (např. Kvaček, 2007). Velkou výhodou těchto na taxonomickém přístupu založených metod je však možnost jejich aplikace na všechny typy společenstev kenofytika, přičemž lze do sledovaných souborů zahrnout jak listy, tak pylové nálezy, jak lze demonstrovat na příkladu příbuzné metody CoA (*coexistence approach*) (Mosbrugger a Utescher, 1997). Druhý, podstatně sofistikovanější, oproti tomu bere v úvahu vztah mezi morfologickými vlastnostmi vybraných rostlinných orgánů, především jejich listů, a okolními klimatickými podmínkami. Předpokládá v tomto směru shodné charakteristiky u rostlin vyskytujících se v obdobném prostředí bez ohledu na jejich taxonomické zařazení a také stálost tohoto vztahu v čase, respektuje tedy známý princip aktualitu (MacGinitie, 1969; Parkhurst a Loucks, 1972; Wolfe, 1979; Wolfe, 1993; Wolfe, 1995; Wing a Greenwood, 1993; Wilf, 1997). Sem patří zejména metoda LMA (*leaf margin analysis*), založená na univariační statistické metodě, která pracuje s poměrem taxonů s celokrajnými listy ve sledovaném souboru (Bailey a Sinnott, 1915; Wolfe, 1979; Greenwood, 1992; Wing a Greenwood, 1993; Wilf, 1997; Wilf a kol., 1998). Složitější je technika CLAMP (*Climate Leaf Analysis Multivariate Program*), sledující velké množství morfologických charakteristik listů příslušných rostlin, které následně porovnává prostřednictvím multivariační statistiky s rozsáhlými databázemi recentních společenstev (Wolfe, 1993; Wolfe, 1995; Wolfe a Spicer, 1999; Teodoridis a kol., 2011). Všechny tyto metody umožňují stanovit relativně přesně lokální klimatické podmínky v minulosti, byť se jejich výsledky často poněkud liší (viz. „*riparian effect*“ – Teodoridis, 2004). Mezi posledně jmenované morfologické metody lze zařadit také tu stanovující hmotnost listu na jednotku jeho plochy (*Leaf mass per area*, $M_A$), která je u stálezelených, neopadavých dřevin vyšší než u tenkolistých, opadavých, a která indikuje spíše aridní, sušší klima (Royer a kol. 2007).

## 1.2 Klasifikace jednotlivých typů interakcí

Klasifikace jednotlivých typů interakcí rostlin a hmyzu i ostatních členovců vychází z konceptu tzv. funkčně potravních skupin (*Functional feeding groups;* zkráceně *FFGs*). Ten byl původně vytvořen pro potřeby ekologických studií sladkovodního hmyzu (Cummins a Merritt, 1984), se nakonec rozšířil i na popis způsobu přijímání potravy u terestrického hmyzu (Lawton a kol., 1993). Jednotlivé klasifikace se u různých autorů, ba dokonce i u jednoho a toho samého autora poněkud liší, ale jen v detailech, základ spočívající v seskupení

jednotlivých typů poškození (*Damage types*) do několika jasně vymezených *FFG* zůstává stejný (Labandeira 1998a, 2001, 2002, 2006; Labandeira a kol., 2007). Odlišné typy poškození (*DT*) jsou definovány svou velikostí, tvarem, počtem a lokalizací na rostlinném orgánu (Labandeira, 1998b; Labandeira a kol., 2007). Důležitou okolností je fakt, že nejsou spojovány s nějakým konkrétním původcem. Jejich kategorizace je tak víceméně abstraktním konstruktem, sloužícím hlavně kvantitativní analýze za účelem paleoenvironmentálních komparativních studijí. Funkčně potravní skupiny (*FFGs*) odpovídají v zásadě způsobu, jakým hmyz nebo jiný členovec intereaguje s rostlinou a také tomu, jaký z toho vzniká vnější efekt. Představují tak jakési sběrné skupiny pro různé typy poškození, která spolu sdílejí nějakou společnou, obecnou, podstatnou charakteristiku. V této práci byl adoptován systém z díla Labandeira a kol. (2007) včetně následných doplňků.

Jednotlivé sběrné skupiny resp. *FFG* užité zde jsou proto rozčleněny následujícím způsobem. **1)** žír okrajový (*Margin feeding*); **2)** žír dutinový (*Hole feeding*); **3)** žír kostrový (*Skeletonization*); **4)** povrchový žír (*Surface feeding*); **5)** tvorba hálek neboli entomocecídií (*Galling*); **6)** minující žír (*Mining*); **7)** tvorba vpichu s následným sáním (*Piercing and sucking*); a nakonec ještě jedna neherbivorní asociace, a to **8)** kladení vajíček (*Oviposition*)[1].

Pro správnou klasifikaci je třeba brát v úvahu i diferenciální diagnózu, neboť řada poškození spadajících do výše uvedených kategorií jeví nápadnou podobnost s výslednými projevy činnosti jiných organismů než je hmyz, resp. členovci. Řada houbových afekcí se šíří koncentricky s vlastním pletivem houby po obvodu a nekrotickým středem, čímž imitují kupříkladu dutinový žír s reakčním lemem. Řada hub také indukuje tvorbu hálkám podobných útvarů, které nápadně připomínají ty vytvářené hmyzem. Důležitým vodítkem jsou proto recentní ustálené asociace hostitelských rostlin s určitými hmyzími původci specifických typů poškození. Dále existují ještě funkčně potravní skupiny, které však již nejsou detekovatelné coby klasické ichnofosilie. Jsou to hlavně povrchové sání (*Surface fluid feeding*), opylování *(Pollination*) a palynovorie *(Palynovory*). Na existenci prvních dvou lze usuzovat takřka výlučně jen nepřímo, podle specializovaných rostlinných orgánů vzácně se vyskytujících u některých fosilních rostlin (Fahn, 1979) a dále podle specificky utvářeného ústního ústrojí (popř. jiných morfologických adaptací) v případě fosilního hmyzu (Labandeira, 1997). Palynovorii lze prokázat ve střevním obsahu (*Gut content*) fosilizovaného hmyzu nebo v koprolitech díky přítomnosti chakteristických pylových zrn (Krassilov a Rasnitsyn, 1997).

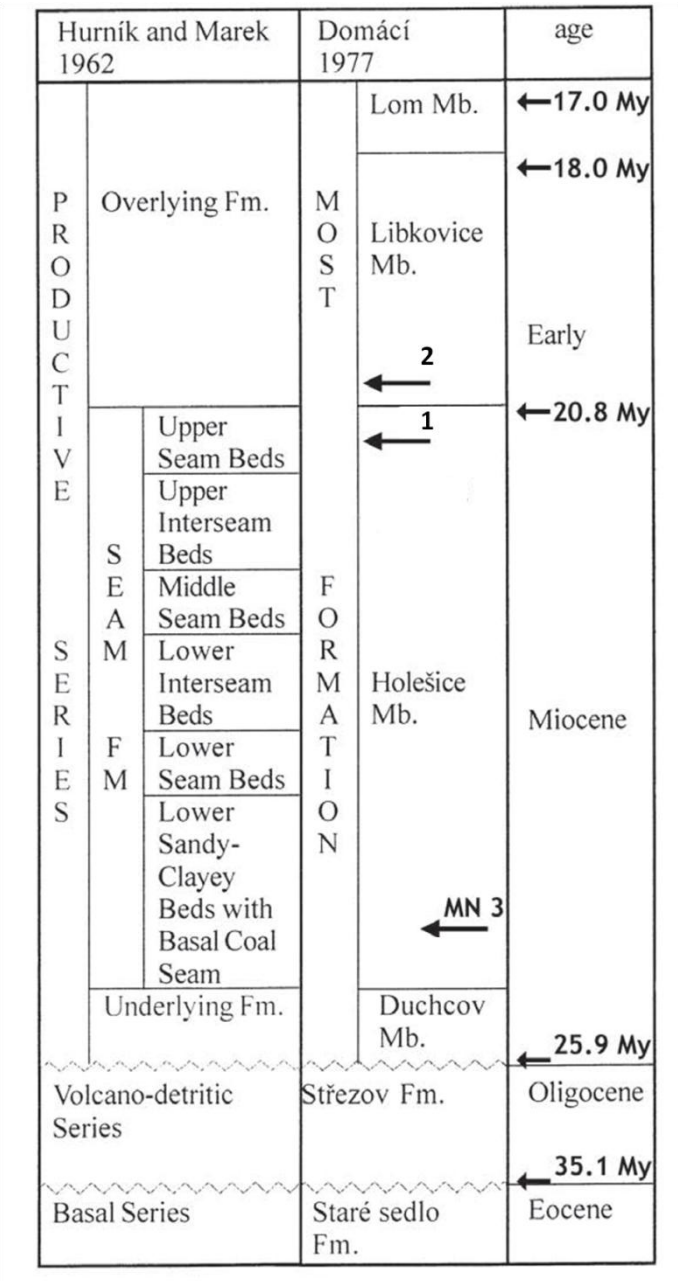
[1] V přiložených publikacích se však jejich vzájemné pořadí od tohoto může lišit.

# 2 Mostecká pánev

## 2.1 Geologie a stratigrafie

Mostecká pánev, dříve zvaná též Severočeská hnědouhelná pánev, představuje největší a také nejdůležitější podkrušnohorskou pánev. Nalézá se v severozápadních Čechách, kde je na západě ohraničena Doupovskými horami, Krušnými horami na severu a Českým středohořím na jihovýchodě. Představuje až 550 m mocný, sedimentární a vulkanoklastický komplex, pokrývající rozlohu 870,3 km$^2$ (Kvaček a kol., 2004). Na příčinu vzniku a vyplňování tohoto rozsáhlého geomorfologického útvaru však přes intenzívní výzkum v této oblasti panují rozdílné názory (Pešek a kol., 2010). Z lithostratigrafického hlediska lze vyplňování mostecké pánve rozdělit na tři samostatné etapy, oddělené hiáty, kterým odpovídají její následující hlavní souvrství – **starosedelské**, **střezovské** a **mostecké** (Shrbený a kol., 1994). Ukládání nejstaršího **starosedelského souvrství** započalo ve středním eocénu a pokračovalo až do počátku oligocénu. Je tvořeno klastickými terestrickými sedimenty. Vznik prostředního, **střezovského souvrství**, je úzce spjat s rozsáhlou vulkanickou činností, probíhající s velkou pravděpodobností po větší část trvání oligocénu. Nejmladší **mostecké souvrství** se započalo vytvářet ve svrchním oligocénu (chatt) a jeho utváření probíhalo až do spodního miocénu (burdigal). Při jeho tvorbě byly výlevy vulkanitů a ukládání pyroklastik střídány vrstvami písčitých a jílovitých říčních i jezerních sedimentů. Toto souvrství se rozděluje do několika dalších vrstev uloženin. Nejstarší jsou **duchcovské vrstvy** (chatt až aquitan), dosahující místy mocnosti až 140 m, které jsou díky svému komplikovanému vývoji z petrografického hlediska nejpestřejší jednotkou mosteckého souvrství (Pešek a kol., 2010). Duchcovské vrstvy se vyznačují heterogenní směsí rostlinných souborů, z nichž některé mají zřetelně teplomilný ráz. Charakteristická je zejména asociace datlovníku a břestovce (*Phoenix – Celtits lacunosa*) *sensu* Kvaček a Bůžek (1982). Jako další příklad paleofloristické asociace lze uvést rovněž nález z vrtu JZ-44 (Jezeří), který zahrnuje vavřínovité *Laurophyllum* sp. div. v kombinaci s borovicí a olší *Pinus* sp. a *Alnus julianiformis*. Z podloží sloje v bývalém lomu Marianna je popsána vodní slanomilná asociace bylin *Cladiocarya-Limnocarpus*, zatímco monotónní asociace dubu porýnského (*Quercus rhenana*) je typická pro centrální část pánve. Na lokalitě Čermníky na Pětipesku se v podloží spodní sloje vyskytují ojedinělé nálezy fytostratigraficky nevýznamných elementů, jako jsou tisovec *Taxodium dubium*, jilm *Ulmus pyramidalis* nebo ambroň *Liquidambar europaea* (Pešek a kol., 2010). Následují **holešické vrstvy** (svrchní chatt až aquitan), tvořené hlavní uhelnou slojí (mocnost místy až 70 m), do které zasahují

střídavě deltové a aluviální jíly až písky. Součástí těchto vrstev jsou i uloženiny tzv. **„žatecké“** a „**bílinské delty“**, obsahující řadu fosiliferních horizontů velmi bohatých na rostlinné zbytky. Na holešické vrstvy naléhají **vrstvy libkovické** (burdigal), které již reflektují zánik uhlotvorby na území Severočeské uhelné pánve. Jsou pro ně charakteristické jezerní uloženiny, jejichž součástí je také ne příliš mocný komplex jílů u Břešťan na Bílinsku označovaný jako **břešťanské jíly** (Pešek a kol., 2010). Celý komplex mosteckého souvrství pak zakončují nejsvrchnější **lomské vrstvy** (svrchní burdigal).




Obr. 1. Stratigrafie Mostecké pánve s naznačenými úrovněmi studovaných lokalit (podle Kvaček a Hurník, 2000), hodnotami paleomagnetického datování (Bucha a kol., 1987) a počátku savčí zóny MN 3 (lokality Ahníkov a Tuchořice – Fejfar 1989). 1. Důl Bílina – horizont No 1, 2 “břešťanské jíly”. Podle Teodoridise (2010).

## 2.2 Paleoekologie holešických a libkovických vrstev

Z hlediska této práce jsou ze zmíněných vrstev mosteckého souvrství podstatné zejména dvě, a to holešické a libkovické. Starší **holešické vrstvy** se vyznačují velmi diverzifikovanou flórou. Její charakter a vegetační ráz jsou určovány především vazbou na uhelnou sloj na Teplicku a „deltové“ sedimenty na Žatecku a Bílinsku. Poněkud chudší z hlediska druhového spektra je skladba rostlinstva uhelných lávek, které dominují nálezy tisovcovitých jehličnanů druhů *Glyptostrobus europaeus, Taxodium dubium, Quasisequoia couttsiae* v asociaci s dalšími bažinnými prvky rozmanitých druhům jako jsou *Stratiotes kaltennordheimensis, Spirematospermum wetzleri, Myrica* sp. div., *Calamus daemonorhops, Salvinia* sp., *Sparganium* sp. div. a jiné (Pešek a kol., 2010). Mnohem bohatší je pak flóra vázaná na slojové proplástky, která kromě karpologických dokladů zahrnuje také rozsáhlý listový materiál. Je zastoupená na řadě lokalit, reprezentujících především oblasti bývalé „žatecké“ a „bílinské delty“. Nejbohatší z nich představují Čermníky na Pětipesku, které poskytuji nálezy stratigraficky vázané na proplástek mezi střední a svrchní lávkou sloje. Pro tuto lokalitu je charakteristická kombinace pánevní vegetace, zastoupená zejména různými společenstvími s rodem *Glyptostrobus* spolu s asociací *Nyssa-Taxodium sensu* Kvaček a Bůžek (1982) a elementy lužního lesa – asociace *Parrotia-Ulmus pyramidalis sensu* Kvaček a Bůžek (1982). Vyskytují se zde také četní zástupci čeledi Lauraceae, dále *Comptonia difformis, Quercus rhenana* a *Ulmus pyramidalis*. Hojné jsou i dřeviny sušších stanovišť, např. *Podocarpium podocarpum, Zelkova* sp. a *Fagus saxonica* – lokalita Přívlaky (Pešek a kol., 2010). Velmi rozsáhlé výzkumy byly realizovány rovněž v souvislosti s flórou **„bílinské delty“** z těsného nadloží uhelné sloje (např. Bůžek a kol., 1992; Boulther a kol., 1993; Kvaček, 1998; 2000; Sakala, 2000; Kvaček a kol., 2004). Charakter složení místní paleoflóry odpovídá zhruba poměrům zjištěným ze „žatecké delty“. Navíc zde byla zaznamenána celá řada akvatických, vesměs vymřelých endemitů, např. *Elephantosotis dvorakii, Hydrochariphyllum buzekii* a *Schenkiella crednei.* Přítomny jsou rovněž bažinná kapradina rodu *Blechnum*, cypřišovitá *Tetraclinis,* teplomilné listnáče *Engelhardia* a *Platanus neptuni* i sabaloidní palma. Celkem bylo z této oblasti popsáno na 110 různých rostlinných taxonů z 65 fosiliferních horizontů. Pro různé horizonty jsou charakteristické různé typy asociací, což odráží složitou dynamiku místních geomorfologických poměrů a na ně navazující změny bioty. To ostatně platí pro celé sedimentační těleso mostecké pánve Zřejmě nejpropracovanější souhrn a přehled ohledně jednotlivých sedimentačních fází mostecké pánve poskytuje práce Mach a kol. (2014). Tato studie jich rozlišuje celkem šest v následujícím pořadí – **(i)** *The central River phase* (A+B);

(**ii**) *The Floodplain and First Moore phase*; (**iii**) *The Whole Basin Swamp phase*; (**iv**) The *Local Lake phase*; (**v**) *The Whole Basi Lake phase*; a poslední (**vi**) *The Swamp Rehabilitation phase*. Podrobně se přitom zabývá postupnou sukcesí jednotlivých floristických asociací v rámci každé z nich. Sedimentační procesy „bílinské delty" přitom začleňuje do fáze č. 4 (*The Local Lakes phase*), umístěné do svrchní části holešických vrstev. **Libkovické vrstvy** se pak kryjí s následující 5. fází (*The Whole Basin Lake phase*). Do rozhraní obou výše uvedených fází jsou pak situovány **břešťanské jíly** [2] **,** známé svým diverzifikovaným rostlinným společenstvím (Teodoridis a Kvaček, 2006). Břešťanská flóra se skládá hlavně ze zástupců jehličnaté čeledi Cupresaceae s. l. (rody *Taxodium*, *Glyptostrobus* a *Quasisequoia*) a opadavých listnatých stromů (*Cercidiphyllum crenatum*, *Nyssa bilinica*, *Craigia bronii*, *Alnus julinaniformis*, *Quercus rhenana*, *Acer tricuspidatum*) typických pro pánevní oblast, doplněné o mezofytní elementy vázané v některých případech na kyselejší biotopy (*Pinus*, *Daphnogene polymorpha*, *Laurophyllum* spp., *Podocerpium*, *Liquidambar*, *Parrotia*, *Zelkova*, *Myrica*, *Acer angustilobum*, *A. integrilobum*, *Fraxinus bilinica*, *Trigonobalanopsis*). Nejsvrchnější lomské vrstvy odpovídají fázi č 6 (*The Swamp Rehabilitation phase*), přičemž je pro ně typická bažinná flóra s rody *Salvinia*, *Azolla*, *Hemitrapa*, *Decodon*, *Potamogeton*). Zastoupeny jsou rovněž jehličnany *Quasisequoia* a *Glyptostrobus* spolu s listnáči *Nyssa gmelinii* a *Myrica undulatissima* (Pešek a kol., 2010; Mach a kol. 2014).

Na základě rozboru řady vybraných charakteristik rostlinných souborů coby paleoklimatických proxy byly pro jednotlivé lokality a tím i vrstvy rámcově stanoveny odpovídající klimatické poměry (např. Teodoridis a kol., 2006; Teodoridis a kol., 2011)

Součástí paleozoologického výzkumu mostecké pánve je také studium její entomofauny, která je zde zastoupena téměř třemi sty fosilními nálezy Dosud byli identifikování zástupci celkem 31 čeledí náležejících do jedenácti hmyzích řádů (Prokop, 2003). Překvapivě převažují zejména zástupci terestrického hmyzu, hlavně mravenci (Hymenoptera: Formicidae) a brouci (Coleoptera), zjevně allochtonního původu. Hojně zastoupen je i vodní hmyz (Odonata; Plecoptera; Coleoptera: Hydrophilidae, Dytiscidae). Nálezy jsou tvořeny hlavně kompresními fosíliemi. Jen ve výjimečných případech, kdy nedošlo k prostorové deformaci, se jedinci nebo jejich zbytky uchovali v třírozměrném stavu (např. silně sklerotizované krovky brouků čeledi Hydrophilidae). Dochované hmyzí fosílie představují nepochybně jen nepatrný zlomek tehdejší druhové rozmanitosti této skupiny. Navíc jsou mezi nimi disproporčně zastoupeny spíše větší druhy s větším fosilizačním potenciálem.

[2] V tomto pojetí se tato studie liší od předchozích, které „břešťanské jíly" kladou do spodní části libkovických vrstev (např. Domácí, 1975; Pešek a kol. 2010).

# 3 Cíle práce

Tato práce měla tři hlavní cíle, které v zásadě odpovídají zaměření hlavních proudů výzkumů týkajících se interakcí členovců a rostlin jako takových. V prvním případě se tak jedná o porovnání rostlinných souborů z lokality dolu Bílina (uloženin „bílinské delty“ s těmi z lokality Břešťany (břešťanské jezerní jíly) z hlediska diverzity a četnosti jejich interakcí se členovci. Vzhledem k tomu, že jsou z obou lokalit přibližně známy tehdejší klimatické poměry, zjištěné na základě paleobotanických proxy dat metodami CLAMP, CoA a LMA, bylo záměrem ověřit, do jaké míry budou či nebudou výstupy ohledně interakcí v souladu s teoretickými předpoklady i empiricky zjištěnými vztahy ve smyslu působení detekovatelných klimatických změn. Jinými slovy, zda je například paleobotanickými proxy daty indikovaný teplotní vzestup v tomto případě doprovázen rovněž vyšší diverzitou a četností vybraných typů interakcí resp. indikovaný pokles teplot doprovázen efektem opačným. Totéž pak analogicky u srážkových poměrů, v jejichž případě kupříkladu u tvorby hálek je předpokládaná korelace právě opačná. V případě rozporu s očekávaným zjištěním pak následným cílem bylo nalézt alternativní vysvětlení tohoto jevu.

Druhým cílem bylo porovnání diverzity a četnosti herbivorie v rámci jednotlivých taxonů napříč svrchními uloženinami holešických vrstev, a to v kontextu zjištěných morfologických charakteristik jejich listoví (např. $M_A$), opět s ohledem na potvrzení nebo vyvrácení předpokládaných korelací. V tomto případě byly zahrnuty společně obě lokality, jak oblast bílinské delty, tak uloženiny břeštanských jílů.

Třetím a posledním, avšak neméně důležitým cílem bylo určení vybraných specifických typů poškození, zejména různých hálek, minujícího žíru ale i vzácných interakcí jiného než herbivorního původu, například ovipozice. Smyslem bylo ověření předpokladu relativní evoluční stálosti zmíněných interakcí prostřednictvím jejich taxonomického zařazení k recentím skupinám původců. V případě hálek byl tento přístup provázán s využitím kvantitativní analýzy jejich výskytu za účelem ověření jejich výpovědní hodnoty o změnách klimatických a dalších environmentálních podmínek ve smyslu v úvodu rozebíraných postulátů.

# 4 Materiál a metodika

Tato práce navazuje na některé předcházející výzkumy interakcí rostlin a členovců v mostecké lokalitě. Jako příklad lze uvést práci Prokopa a kol (2010), pojednávající o této problematice již v intencích moderního přístupu, respektujícího členění výše uvedených asociací do jednotlivých funkčně potravních skupin sdružujících podobné typy poškození (viz Labandeira a kol., 2007). Jako další příklady lze uvést ichnofosílie pravděpodobně způsobené dřevokazným hmyzem, nebo ichnorod *Lamniporichnus* diagnostikovaný na peckách miocénního břestovce (Mikuláš a Dvořák, 1999; Mikuláš a kol., 1998). O konkrétních příkladech hálek z této lokality se zmiňuje i Titchener (1999), nicméně je neklasifikuje do výše uvedených kategorií, ani se nesnaží o bližší taxonomické určení jejich původců.

Zde pojednávaný a studovaný materiál se nachází ve dvou institucionálních sbírkách. V paleontologických sbírkách Národního muzea v Praze se nachází materiál z již zaniklé lokality Břešťany a v depozitáři geologické sekce akciové společnosti Severočeské doly v Bílině jsou deponovány nálezy z bývalé „bílinské delty“. Výzkum herbivorních asociací z hlediska jejich kvantitativní analýzy byl zaměřen výhradně na kompresní fosílie listů dvouděložných rostlin. Ty dohromady čítají soubor 3509 otisků. Za účelem porovnání prostředí bílinské delty s nálezy břeťanských jezerních jílů byl tento soubor dále rozdělen na dva odpovídající podsoubory, čítající 2233 resp. 1260 otisků listů. Zbývajících 16 listů nebylo do srovnání výše uvedených prostředí zahrnuto, neboť se jedná o nálezy z podloží „bílinské delty“. Do porovnání četnosti a diverzity interakcí v rámci vybraných taxonů napříč holešickými vrstvami však již zahrnuty byly. Jednotlivé otisky byly studovány z hlediska taxonomické příslušnosti, stratigrafické pozice, přítomnosti projevů sledovaných interakcí a také $M_A$ (*Leaf mass per area*) původních listů. Při studiu specifických typů poškození, tedy hálek a minového žíru byl soubor rozšířen o soubor 133 otisků jehličnanu druhu *Taxodium dubium*.

Za účelem kvantitativní analýzy byly jednotlivé typy poškození determinovány na základě své velikosti, tvaru, počtu a pozice na čepeli listu za využití manuálu, který obsahuje práce Labandeira a kol. (2007). Dle stejného klíče pak byly detekované jednotlivé typy poškození (DT) rozřazovány do osmi příslušných funkčně potravních skupin (FFG). V této studii jsou rozlišovány následující FFG: (**i**) dutinový žír (*Hole feeding*), (**ii**) okrajový žír (*Margin feeding*), (**iii**) povrchový žír (*Surface feeding*), (**iv**) kostrový žír (*Skeletonization*), (**v**) tvorba hálek (*Galling*), (**vi**) minující žír (*Mining*), (**vii**) tvorba vpichu s následným sáním (*Piercing*

*and sucking*) a (**viii**) kladení vajíček (*Oviposition*). Zvláštní kategorii jdoucí napříč všemi vyjmenovanými funkčně potravními skupinami představují tzv. speciální typy poškození (*specialized types of damage*), zahrnující typy poškození mající velmi úzký okruh potenciálních původců (Wappler, 2010). Pozornost byla věnována i zachycení jakýchkoli jiných forem interakcí členovců a rostlin než jsou výše uvedené typy poškození, což nakonec vyústilo v objevení jedné unikátní asociace. Z důvodů diferenciální diagnózy a pomoci při stanovování paleoekologických podmínek byly rovněž studovány a diagnostikovány jiné než členovčí asociace, např. projevy houbových afekcí. Pro taxonomické určení specifických typů poškození, zejména hálek a min za účelem jejich komplexního porovnání s možnými recentními protějšky, byla nutná detailní morfologická analýza spolu s podrobnější revizí systematické příslušnosti hostitelské rostliny.

Stanovení hmotnosti na plochu listu ($M_A$) pak probíhalo tak, že bylo nutné změřit šířky petiolu a celkovou plochu listu na digitálních fotografiích otisků listů. List musel mít kompletní petiolus se zřetelnými okraji a nepřerušeným spojením s čepelí. Pokud nějaká její část chyběla, například v důsledku okusu, musel jít obrys listu snadno zrekonstruovat, jinak jej nebylo možno použít. K měření byla využita volně dostupná aplikace Image J (http://rsb.info.nih.gov/ij). Pro stanovení vlastní hmotnosti na plochu listu u jednotlivých fosílií, byl použit výpočet podle protokolu Royer a kol. (2007).

Z důvodů nutnosti porovnání diverzity mezi nestejně velkými podsoubory „deltového horizontu“ a „břeštanských jílů“ a stejně tak mezi různě početně zastoupenými taxony v rámci souboru celkového bylo nutné provést rarefakce na shodný počet příslušný entit v rámci příslušných souborů a podsouborů. V případě taxonů se pak jednalo o ty, zastoupené počtem 25 a více exempláři. Specifickým úkonem byla tvorba rarefakčních křivek, dokumentujcím postupný nárůst diverzity v závislosti na přibývajícím počtu listů resp. výskytů poškození.

Proces rarefakce je založen na náhodném, opakovaném a mnohačetném výběru stanoveného počtu sledovaných entit a následném stanovení odpovídajícího stupně diverzity v takto získaném vzorku spolu s příslušnou hodnotou směrodatné odchylky. Při konstrukci rarefakcích křivek se tento postup postupně opakuje vždy pro jiný, o určitý nárůst příslušných entit (v tomto případě listů nebo výskytů sledované kategorie poškození nebo funkčně potravní skupiny) vyšší vzorek. V této práci byly užity dvě varianty této techniky. První je rarefakce bez opakování („*Resampling without replacement“*), modifikovaná podle Wappler, (2010). Tato metoda je poněkud zatížena efektem zmenšujícího se rozptylu v náhodně vygenerovaných výběrech v případě, že se počet rarefikovaných entit blíží jejch celkovému počtu v souboru (Coleman 1981). Naopak výhodou metody je realistický odhad očekávané

diverzity pro danou velikost výběru. Variabilita výběrů však ve středních částech takto získané rarefakcí křivky relativně stabilizovaná a tyto hodnoty pak lze užít k případnému porovnávání výsledků v rámci odlišných souborů, aniž by došlo k ovlivnění výše popsaným zkreslujícím efektem. Za účelem testování signifikance zjištěných rozdílů úrovně interakcí mezi „bílinskou deltou a „břešťanskými jíly“ byla aplikována i druhá varianta rarefakce, spočívající v náhodných výběrech s opakováním („*Resampling with replacement*“). Tato metoda sice poněkud podhodnocuje odhadnutou střední hodnotu diverzity, avšak variabilita se kontinuálně nezmenšuje s rostoucím poměrem velikosti výběru k základnímu souboru jako u modifikovaných rarefakčních křivek (Gotelli a Colwell, 2001). Pro stanovení příslušných úrovní diverzity typů poškození v rámci vybraných vybraných kategorií (tj. funkčně potravních skupin i taxonů) byly užity obě metody, přičemž výše zmíněné diverzity byly rarefikovány jak na počet listů, tak na počet vlastních výskytů v daném (pod)souboru. Výskytem určitého typu poškození se rozumí skutečnost, že se na čepeli listu vyskytuje alespoň jeden jeho projev. To znamená, že nezáleží na tom, zda je na listu přítomno pět nebo třeba deset hálek, nebo zda na jeho povrchu zejí tři nebo pět otvorů způsobených dutinovým žírem.

Další testovanou kategorií byly rozdíly v procentu zasažených listů v rámci jednotlivých funkčně potravních skupin mezi soubory ze dvou inkriminovaných vrstev i mezi jednotlivými taxony ($N \geq 25$). Důležitou (byť netestovanou) kategorií, kterou bylo rovněž nutno stanovit, byl proporcionální výskyt poškození v rámci té které kategorie vztažený na jeden list. Tedy počet výskytů jednotlivých typů poškození v dané kategorii resp. funkční potravní skupině dělený počtem všech listů souboru nebo příslušného taxonu. Pro celý výchozí soubor listů byl rovněž stanoven počet listů zasažených jedním, resp. dvěma, třemi nebo čtyřmi typy různých poškození, náležejícím do jedné, resp. dvou nebo tří funkčně potravních skupin. Jednotlivé typy testů a snimi související odkazy na užitou literaturu jsou pak uvedeny v metodice příslušných publikací. Pro veškeré analýzy dat bylo užito statistického prostředí programovacího jazyka R, verze 2.10.0 (R Development Core Team, 2009), přičemž některé procedury využívaly kromě základních balíčků (*Package*) také balíček Vegan (Oksanen a kol. 2010) a balíček Design (Harell 2009).

Přístrojové vybavení pro detailní výzkum morfologie specifických typů interakcí za účelem jejich bližšího taxonomického určení zahrnovalo následující položky – binokulární mikroskop Leica MZ16, optický mikroskop Olympus a fotoaparát Canon D550 s reverzním objektivem MP-E 65 mm nebo makro objektivem EF-S 60 mm. Všechny pořízené fotografie byly dále zpracovány v grafickém programu Adobe Photoshop 8.0.

# 5 Shrnutí výsledků a diskuze

Pokud jde o rozdíly v dosažené četnosti a diverzity interakcí rostlin a členovců mezi společenstvími „bílinské delty“ a „břešťanskými jíly“ bylo zjištěno následující. Uloženiny „bílinské delty“ mají vyšší procento poškozených listů a navíc i vyšší zastoupení poškozených listů s více než jedním typem poškození. Rozdíl v proporcionálním výskytu jednotlivých typů poškození (Dt/List) je z tohoto důvodu ještě o něco vyšší než je tomu v případě procenta zasažených listů. Oba soubory se rovněž významně liší co do zastoupení jednotlivých funkčně potravních skupin. Uloženiny „bílinské delty“ vykazují podstatně vyšší incidenci dutinového, kostrového žíru a povrchového žíru než „břešťanské jíly“, které se naopak naopak vyznačují čtyřnásobnou frekvencí výskytu tvorby hálek.

Srovnání diverzity vybraných kategorií poškození rarefikované na počet listů[3] v rámci celého souboru a v rámci všech taxonů přítomných v počtu 25 a více listů zároveň v obou uloženinách ukázalo, že všechny takto získané výsledky vykazují vyšší absolutní hodnoty ve prospěch „deltových“ uloženin. Statisticky testované signifikantní rozdíly byly nicméně potvrzeny pouze v některých případech. Pro celé soubory to byly diverzity všech typů poškození a funkčně potravních skupin, pro soubory stávajících jen z výše uvedených taxonů po separaci vlivu jejich autekologie a interspecifické variability pak pouze diverzity všech typů poškození, specializovaných typů poškození a tvorby hálek. Poněkud jiný obraz poskytlo srovnání diverzity vybraných kategorií poškození rarefikované na počet vlastních výskytů[4], opět v rámci celého souboru i v rámci taxonů zastoupených počtem 25 a více listů přítomných v obou uloženinách. Zde byl v obou výše uvedených kategoriích statistickým testováním potvrzen signifikantní rozdíl pouze v diverzitě specializovan typy poškození, opět ve prospěch uloženin „bílinské delty“.

Při posuzování vlivu $M_A$ (*Leaf mass per area*) na incidenci výskytu sledovaných funkčně potravních skupin v rámci odlišných společenství „bílinské delty“ i „břešťanských jílů“ je možné konstatovat, že s výjimkou signitifikantního poklesu dutinového žíru provázející nárůst $M_A$ v prvním případě, nebyla u zbývajících kategorií poškození shledána v tomto směru žádná

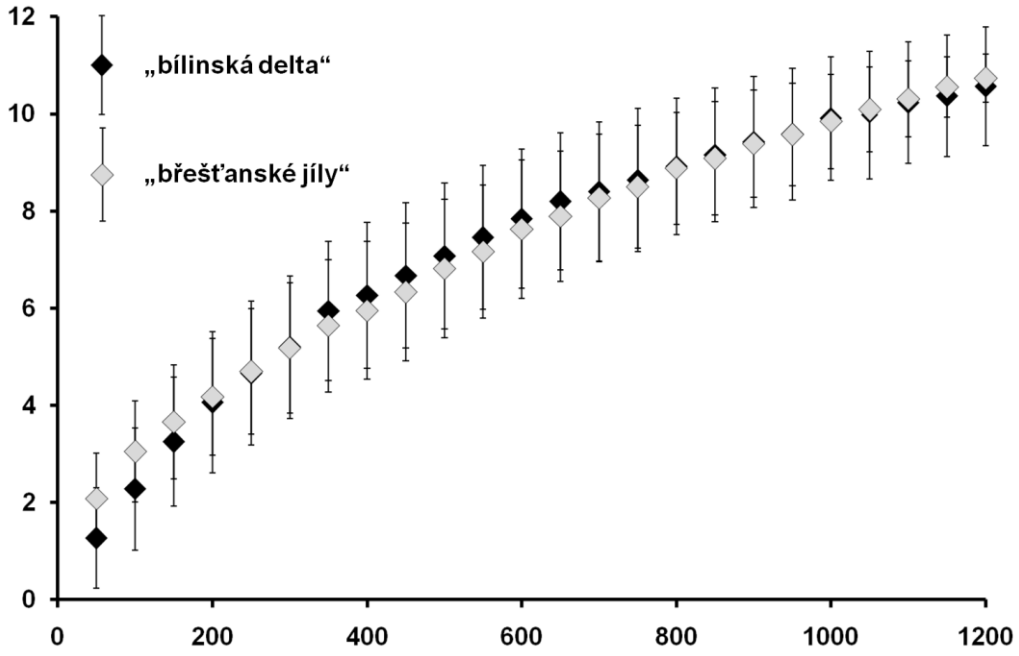
[3] Jednalo se o (**i**) všechny typy poškození, (**ii**) funkčně potravní skupiny jako takové, (**iii**) specializované typy poškození, (**iv**) tvorbu hálek a (**v**) minující žír. V případě celéch souború byly příslušné diverzity rarefikovány na 100 listů; v případě vybraných taxonů (N≥25) pak na oněch 25 listů.

[4] Jednalo se o (**i**) všechny typy poškození, (**ii**) funkčně potravní skupiny jako takové, (**iii**) specializované typy poškození a (**iv**) tvorbu hálek. V případě celéch souború byly příslušné diverzity rarefikovány na 20 výskytů; v případě vybraných taxonů (N≥25) pak na pět výskytů příslušné kategorie poškození.

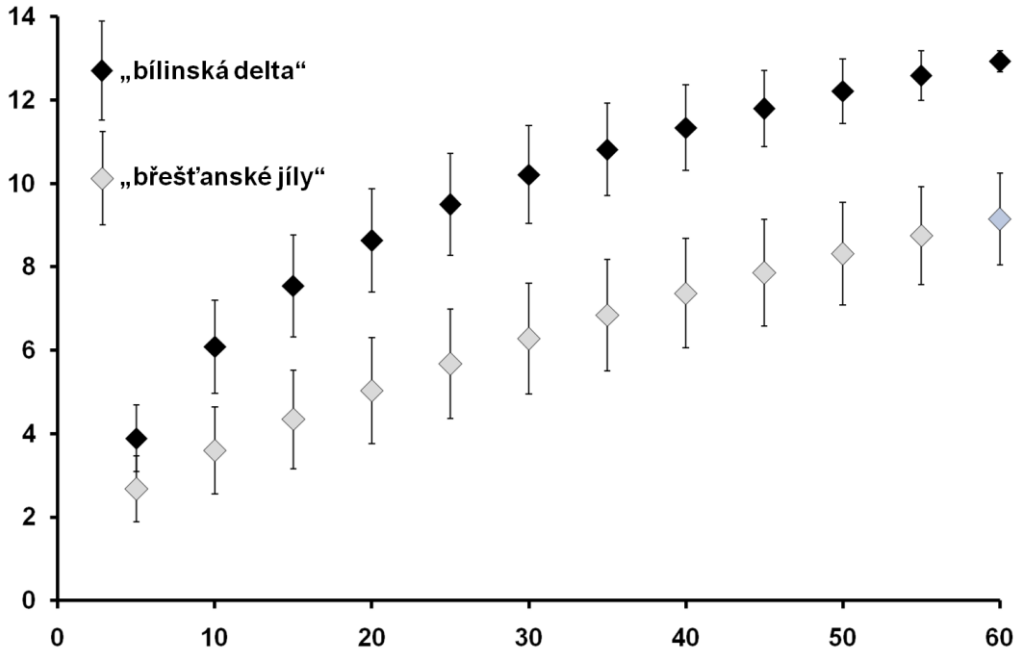
pozitivní či negativní korelace. Samotná průměrná hodnota $M_A$ pak byla v rámci souboru „břešťanských jílů“ přeci jen o něco vyšší, byť statisticky nepříliš průkazně.

V souvislosti s hodnotami rarefakcí coby vstupními daty ke statistickému testování průkaznosti zjištěných hodnotových rozdílů je třeba zdůraznit alespoň dvě důležitá zjištění. Především se ukázalo, že se průběhy rarefakčních křivek diverzity příslušné kategorie poškození významně liší v závislosti na tom, zda byly konstruovány na počet listů nebo na počet výskytů jednotlivých poškození dané kategorie (viz metodika). Pro účel porovnání diverzity vybrané kategorie poškození se pak varianta rarefakce na počet listů ukázala jako méně vhodná. Zjištěná hodnota diverzity je totiž výrazně ovlivněna frekvencí výskytu dané funkčně potravní skupiny resp. kategorie poškození ve sledovaném souboru. Může se tak stát, že rarefikovaná hodnota vybrané kategorie poškození je v důsledku jeho vysoké incidence v souboru vyšší než u souboru s incidencí nižší, přesto že s absolutní diverzitou jsou na tom sledované soubory přesně naopak. Z tohoto hlediska je mnohem relevantnější užít jako vstupní data ke statistické analýze a testování výstupní hodnoty rarefakce daného souboru na počet výskytů jednotlivých poškození té které kategorie. I zde je výsledek ovšem ovlivněn mírou ekvitability výskytu různých typů poškození, odpadá však výše uvedené zkreslení. Je s podivem, že celá řada prací nebere tuto skutečnost v potaz a srovnává diverzitu interakcí v rámci zvolených lokalit pomocí rarefakčních křivek konstruovaných na počet listů (např. Wilf a kol. 2005; Wappler, 2010; Wappler a kol., 2012). Takovýto ukazatel v sobě však slučuje dvě obtížně separovatelné informace, jednak tu o vlastní diverzitě a za druhé tu o frekvenci výskytu příslušné kategorie interakce. Interpretace výsledku může být proto poněkud zavádějící. Dalším aspektem, kterému je třeba věnovat zvýšenou pozornost, je volba počtu výskytů jednotlivých typů poškození, na které je třeba rarefikovat při stanovování míry diverzity určené jako vstupní hodnoty do příslušného testování. Pokud se arbitrárně zvolí nízký počet výskytů (platí to i pro méně vhodnou variantu rarefakcí na počet listů), výsledek bude s velkou pravděpodobností neprůkazný. Optimální počet, na který by měla za účelem srovnání diverzit příslušných entit mezi různými soubory rarefakce probíhat, je počet entit v tom nejmenším z nich. Skutečnost, že bylo prokázáno jen málo testy ověřených signifikantních rozdílů v diverzitách poškození napříč různými kategoriemi, zjevně padá na vrub rarefikování vstupních hodnot diverzit na relativně nízký počet příslušných entit. Oba diskutované jevy lze demonstrovat na dvou níže uvedených grafech č. 3 a 4.

Z hlediska průkaznosti testů je také vhodné upřednostnit proporcionální počet výskytů DT dané kategorie (celkový počet výskytů dělený počtem všech listů přísl. souboru), který není




Obr. 2. Znázorňuje průběh rarefakční křivky diverzity tvorby hálek sestrojené ve variantě na počet listů metodou *Resampling without replacement*. Do charakteru křivky se zásadním způsobem promítá skutečnost, že incidence (procento zasažených listů) je v uloženinách „břešťanských jílů“ čtyřnásobná oproti uloženinám „bílinské delty“.




Obr. 3. Znázorňuje průběh rarefakční křivky diverzity tvorby hálek sestrojené ve variantě na počet jednotlivých výskytů té samé funkčně potravní skupiny. Je zřejmé, že reálný rozdíl v diverzitě je mnohem vyšší, než jak indikuje předchozí graf. Rovněž je patrné, že testovat rozdíl příslušné diverzity rarefikované na menší počty výskytů je velmi diskutabilní.

totožný s proporcionálním zastoupením poškozených listů (počet poškozených listů dělený počtem všech listů přísl. souboru). Čím větší je v daném souboru podíl listů s více než jedním typem poškození, tím větší je rozdíl mezi těmito dvěma veličinami. Pokud je tedy srovnávána míra „promořenosti“ souboru např. hálkami nebo jiným typem poškození, pak větší výpovědní hodnotu má ukazatel DT/list, neboť zohledňuje i fakt, že na určitém procentu poškozených listů mohou být přítomny i dva nebo tři různé typy hálek. U min a hálek se tato situace sice vyskytuje jen vzácně (většinou se DT/list = proporcionálnímu zast. pošk. listů), ale u dutinového a okrajového žíru je běžná. V rámci celého souboru pak procento listů zasažených poškozeními z různých i stejných FFG rozhodně není zanedbatelné. Z tohoto je zjevné, že při porovnávání míry incidence jednotlivých FFG mezi dvěma nebo více soubory je porovnání přes DT/list průkaznější. Je to patrné i na grafech týkajících se proporcionálního výskytu jednotlivých funkčně potravních skupin u taxonů dosahujících počtu 25 a více uvedených v přiložených publikacích. Rozdíly mezi porovnávanými uloženinami „bílinské delty“ a „břešťanských jílů“, pokud jde o zjištěná procenta listů zasažených v rámci odlišných funkčně potravních skupin, jsou však natolik průkazné, že jejich testování na tyto hodnoty poskytlo též signitifikantní výsledky a bylo tedy plně postačující.

Porovnáme-li zjištěné výsledky a jejich potenciální implikace pro paleoklimatické podmínky v kontextu známých paleoklimatických údajů zjištěných pro oba typy uloženin pomocí paleobotanických proxy, a uváděných v různých publikacích (Teodoridiss a kol., 2006; Teodoridis a Kvaček, 2006; Teodoridis, 2010, Mach a kol., 2014 – viz také Tab. č. 1), vidíme řadu rozporů. V obou sledovaných aspektech, tj. diverzity i frekvence poškození, vykazuje prostředí „bílinské delty“ vyšší úrovně nežli je tomu v případě „břešťanských jílů“. Detekované diverzity rarefikované na určitý shodný počet, ať již listů nebo výskytů, jsou vyšší ve všech sledovaných kategoriích poškození, byť byl statisticky průkazný rozdíl prokázán (vzhledem k nedostatku, jakým se vyznačuje použitá varianta rarefakcí na počet listů souboru) pouze v případě speciálních typů poškození. Statisticky signifikantní rozdíly ve prospěch „bílinské delty“ lze rovněž vysledovat v případě procenta poškozených listů v rámci všech sledovaných kategorií a funkčně potravních skupin. To samé by v ještě větší míře platilo i pro hodnotu proporcionálního výskytu poškození na list souboru. Jedinou, nicméně velmi podstatnou výjimku představuje tvorba hálek. Všechna tato zjištění by implikovala pro tehdejší prostředí „bílinské delty“ teplejší a vlhčí klimatické podmínky. Prostředí „břešťanských jílů“ by pak na základě těchto výsledků mělo být spíše chladnější a sušší. Paleobotanické výzkumy však svědčí o opaku (Tabulka č. 1). Vysvětlení tohoto rozporu není jednoduché a pravděpodobně zahrnuje vliv mnoha, navzájem se ovlivňujících faktorů. Vyšší

diverzita i frekvence poškození rostlinného společenství „bílinské delty“ může souviset s jeho vyšší taxonomickou rozmanitostí, nicméně také flóra „břešťanských jílů“ byla velmi druhově bohatá. Na druhou stranu, přítomnost zástupců rodu „*Pinus*“ a vavřínovitých rostlin v posledně jmenovaných vrstvách může opravdu indikovat sušší prostředí, nebo alespoň prostředí s nerovnoměrně rozloženými srážkami v čase, čemuž by nasvědčovala čtyřnásobná frekvence výskytu hálek (Fernandes a Price, 1988, 1991; Wright a Samways, 1998; Cuevas-Reyes a kol., 2004). Aridnějšímu prostředí „břešťanských jílů“ také nasvědčuje i vyšší průměrné $M_A$ (*Leaf mass per area*) jejich rostlinného souboru. Je nepochybné, že uloženiny „bílinské delty“ a „břešťanských jílů“ reprezentují dvě odlišná prostředí resp. dva odlišné biotopy, kde se kromě měnících se klimatických podmínek na celkové úrovni diverzity a četnosti sledovaných interakcí podílely i další, obtížně separovatelné vlivy (např. taxonomické složení flóry, nadmořská výška, charakter půdního substrátu, úroveň hladiny podzemní vody, obsah stopových prvků v půdě atp. – Cuevas-Reyes a kol., 2003; Veldtman a McGeoch, 2003). Otázkou zůstává také spolehlivost údajů získaných na základě paleobotanických proxy dat, a které se od sebe dost odlišují (viz např. tzv. „*riparian effect*“, Teodoridis, 2004).

Podobně nejednoznačně dopadlo i porovnání diverzity frekvence poškození v rámci vybraných funkčně potravních skupin mezi jednotlivými taxony zastoupenými v počtu 25 a více exemplářů napříč jednotlivými vrstvami holešického souvrství vč. „břešťanských jílů“. Nejfrekventovanějším poškozením je dutinový žír, následovaný okrajovým žírem a tvorbou hálek. Nejvyšší incidenci (frekvenci) poškození pak vykazují opadavé stromy, jako jsou *Carya* sp. a *Populus zaddachii*. Tenkolisté opadavé dřeviny rodů *Acer*, *Alnus*, *Fraxinus*, *Nyssa* a *Populus* rovněž vykazují nejvyšší diverzitu odlišných typů poškození. Na druhou stranu, stálezelený *Quercus rhenana* se svými tuhými, kožovitými listy dosahuje také relativně vysokou diverzitu poškození. Jinak poskytuje srovnání zjištěných diverzit poškození v rámci vybraných kategorií spíše uniformní výsledky. S vyjímkou několika málo taxonů, vykazujících větší míru poškození jsou rozdíly zejména v dosažené diverzitě velmi malé. V případě divezity všech poškození rarefikované na pět vlastních výskytů byla shledána nepatrná pozitivní korelace s rostoucí frekvencí poškození.

Co se týče taxonomické identifikace některých specifických typů interakcí, úspěšná byla zejména u hálek, celkem u 14 z nich se jejich původce podařilo zařadit do úrovně čeledi a dokonce stanovit nejbližší příbuzný druh. Jako nejzajímavější hálky se jeví ty na větvičce vyhynulého evropského tisovce druhu *Taxodium dubium*, jevící značnou podobnost s dosud nepopsaným druhem rodu *Taxodiomyia* GAGNÉ, 1968, vyskytujícím se na recentním

severoamerickém tisovci druhu *Taxodium distichum* (Gagne, osobní sdělení). Zástupci čeledi bejlomorkovitých (Diptera: Cecidomyidae) jsou po roztočích (Acari) z čeledi vlnovníků (Eriophyidae) druhými nejčastějšími diagnostikovanými původci fosilních hálek ze severočeské pánve, zastoupení celkem pěti různými typy hálek, vyskytujících se na stejném počtu hostitelských rostlin. Vlnovníci jsou nejpočetnější, bylo diagnostikováníо celkem sedm potenciálních původců (stejný počet typů hálek) na pěti druzích hostitelských dřevin. Vzácnější jsou nálezy hálek původců z řad blanokřídlých (Hymenoptera), náležejících do čeledi žlabatkovití (Cynipidae). Podobně jako zástupci řádu Hemiptera z čeledi Phylloxeridae, zanechali po sobě po jednom typu hálky na jedné hostitelské rostlině. Ohledně dalších specifických typů poškození, pravděpodobného původce z čeledi Nepticulidae (řád Lepidoptera) se podařilo identifikovat v případě minujícího žíru na vyhynulé vrbě druhu *Salix haidingeri*. Na listu druhu stejného stromu byla rozpoznána ještě ovipozice, nejspíše od vážek z čeledi Lestidae (řád Odonata). Pozoruhodným nálezem byly hmyzí schránky zbudované výlučně z jehlic již zmíněného druhu tisovce. Jejich taxonomické určení je však nejisté. V zásadě se nabízejí dvě alternativy, přičemž každá má svoje pro a proti. Buď se jedná o původce z řádu chrostíků (Trichoptera), čemuž nasvědčuje charakter prostředí nebo motýla (Lepidoptera) z čeledi Psychidae (charakter uspořádání jehlic). Všechny tyto zjištěné asociace vypovídají o relativně dlouhé koevoluční stázi, trvající od spodního miocénu až dosud, tedy přibližně nějakých 20 miliónů let.

Tabulka 1. Přehled paleoklimatických údajů a paleobotanických proxy metod jejich stanovení

| Lokalita | MAT [°C] | | CMMT [°C] | | WMMT [°C] | | MAP [mm] |
|---|---|---|---|---|---|---|---|
| | CLAMP | CoA | CLAMP | CoA | CLAMP | CoA | CoA |
| Bílina H1[5] | 12.2 (1.3)* | 15.6 | 3.4 (2.6)* | 3.8 | 21.4 (1.7)* | **24.7**–26.4 | **1194** |
| Břešťany[5] | 14.5 (1.1)* | 16.5–18.9 | 8.9 (1.9)* | 4.8–12.2 | 21.1 (1.4)* | **24.7**–27.5 | **1194**–1333 |
| Břešťany[6] | 16.5±1.17 | 16.5–17 | 5.7±1.88 | 9.6–11.7 | 27.2±1.58 | 26.4–26.8 | **1194**–1281 |

| | MAT [°C] | | | | | 3WET | 3DRY |
|---|---|---|---|---|---|---|---|
| | CLAMP | LMA | CoA | | | CLAMP | |
| Břešťany[7] | 17.2 | 22.2 | 14.5–16.6 | | | | |
| Břešťany[8] | 16.5 | | | 5.7 | 27.2 | 81.9 (13.8) | 49.4 (9)* |

[5] Mach, K., Teodoridis, V., Grygar, T.M., Kvaček, Z., Suhr, P., Standtke, G., 2014. An evaluation of the palaeogeography and palaeoecology in the Most Basin (Czech republic) and Saxony (Germany) form the late Oligocene to the early Miocene. Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen 2, 13–45.

[6] Teodoridis, V., Kvaček, Z., Uhl, D., 2006. CLAMP and CA proxy data from the Lower Miocene of North Bohemia. 141. In Teodoridis, V., Kvaček, Z., Kvaček, J. (eds) Abstracts, 7th EPPC, Prague September 6–12, 2006. National Museum, Prague.

[7] Teodoridis, V., 2010. The integrated plant record vegetation analysis of Early Miocene assemblages from the Most Basin (Czech Republic). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 256, 303–316.

[8] Teodoridis, V., Kvaček, Z., 2006. Palaeobotanical research of the Early Miocene deposits overlying the main coal seam (Libkovice and Lom Mbs.) in the Most Basin (Czech Republic). Bulletin of Geosciences 81, 93–113.

# 6 Závěr

Vzájemné porovnání dvou odlišných rostlinných společenstev z prostředí stratigraficky starší „bílinské delty“ a mladších „břešťanských jílů“ v rámci holešických vrstev (depoziční fáze 4 resp. fáze 4/5 sensu Mach a kol., 2014) mosteckého souvrství z hlediska frekvence a diverzity interakcí členovců a rostlin potvrdilo v řadě aspektů podstatné rozdíly. S výjimkou tvorby hálek, jejíž četnost je ve společenstvu „břešťanských jílů“ oproti „bílinské deltě“ čtyřnásobná, vykazuje starší z nich signifikantně vyšší frekvenci všech ostatních sledovaných kategorií poškození a funkčně potravních skupin. V případě diverzity je situace obdobná, hodnoty diverzit rarefikované za účelem srovnání nestejně velkých vzorků obou souborů na shodný počet listů či výskytů jednotlivých poškození jsou, pokud jde o „ bílinskou deltu“, vyšší ve všech sledovaných kategoriích interakcí, byť by signifikantní rozdíl byl statistickými testy potvrzen pouze v případě speciálních typů poškození. Tyto výstupy svědčí pro teplejší a vlhčí klimatické podmínky „bílinské delty“, což ovšem příliš nekoresponduje se zjištěním na základě paleobotanických proxy metodami CLAMP, CoA a LMA. Otázkou však je, nakolik jsou takto zjištěné rozdíly signifikantní, resp. zda byly v tomto smyslu testovány a do jaké míry jsou zatíženy nějakou systémovou chybou. Interpretace těchto rozporů je velmi nesnadná, neboť na frekvenci a diverzně studovaných interakcí se s největší pravděpodobností podílí celá řada navzájem se ovlivňujících faktorů, které od sebe lze jen stěží separovat. Klimatický faktor je tak jen jeden z mnohých, byť možná nejdůležitější.

Ohledně porovnání diverzity frekvence poškození v rámci vybraných funkčně potravních skupin a kategorií poškození mezi jednotlivými taxony zastoupenými v počtu 25 a více napříč sledovanými vrstvami lze konstatovat, že nejvyšší míru postižení vykazovaly tenkolisté opadavé dřeviny. Tento výsledek se dal víceméně očekávat, neboť stále zelené popř. poloopadavé rostliny s vyšším $M_A$ disponující tužšími, kožovitými listy investují vzhledem k jejich delší životnosti více obranných (chemických, mechanických) prostředků nežli ty opadavé.

Pokud jde o identifikaci a taxonomickou determinaci potenciálních původců jednotlivých vysoce specifických afekcí jako jsou miny a hálky, byla určena jich celá řada, a to zejména u hálek. V jejich případě se to podařilo dokonce do úrovně jednotlivých čeledí a rodů, přičemž bylo možné stanovit i možné druhy jejich recentních protějšků. Zjištěné byly i jeden výskyt ovipozice a řada ojedinělých schránkek hmyzu zbudovaných z taxodiových jehlic. Většina

těchto nálezů představuje unikátní nálezy v evropském i celosvětovém měřítku. Všechny pak podávají svědectví o pozoruhodné stálosti těchto koevolučních vztahů v čase.

Na úplný závěr je třeba uvést několik následujících poučení, která se vztahují hlavně ke vzájemnému porovnávání lokalit ohledně diverzity a frekvence sledovaných interakcí. Předně je při vyhodnocování rozdílů v diverzně nutné jako jediný relevantní vstup brát její hodnotu rarefikovanou na shodný počet výskytů poškození v rámci příslušné kategorie či potravně funkční skupiny. Z důvodů následného statistického testování je výše uvedený počet třeba zvolit v náležité výši, nejlépe se řídit nejvyšším počtem výskytů poškození dané kategorie toho nejchudšího souboru. Tedy pokud je v souboru A 10 výskytů, v souboru B 15 výskytů a v souboru C 20 výskytů sledované kategorie poškození, je třeba rarefikovat na deset výskytů, a ne třeba na pět, a to bez ohledu na slabší „sílu“ testu. Jinak hrozí riziko falešně negativních výsledků. Jako doplňující test je vhodné stanovit ekvitabilitu výskytu různých typů poškození ve srovnávaných souborech, tj. jestli jsou zastoupeny rovnoměrně nebo jeden či dva výrazně dominují a zbytek se vyskytuje jen sporadicky. I tento aspekt má podstatný vliv na rarefikované hodnoty diverzit a to i tehdy, je-li zvolena varianta rarefakcí na počet výskytů.

Při vyhodnocování rozdílů ve frekvenci výskytu příslušné kategorie poškození nebo funkčně potravní skupiny má oproti procentu poškozených listů vyšší vypovídající hodnotu proporcionální výskyt poškození dané kategorie vztažený na jeden list souboru, tedy počet výskytů dělený počtem listů souboru, přičemž výskytem se rozumí alespoň jeden projev daného poškození přítomný na listu. Výše uvedený přístup bere v úvahu skutečnost, že na určitém procentu zasažených listů se vyskytují poškození více než jednoho typu. Maximální počet typů poškození ve studovaném souboru dosáhl počtu čtyř, byť se tak stalo pouze v jednom případě.

A poslední (*last but not least*) postřeh vztahující se k interpretačním pokusům ve smyslu propojení klimatických a paleoklimatických aspektů zkoumaného prostředí s kvantitativním vyhodnocováním sledovaných interakcí. Pokud sledujeme výlučně klimatický signál těchto asociací, tj. chceme je využít jako svého druhu paleoklimatická proxy, je třeba zvolit lokality, které si navzájem odpovídají charakterem svého prostředí; to jest nejlépe ty, které reprezentují shodné biotopy. Měly by se také nacházet na pokud možno stejné zeměpisné šířce a ve stejné nadmořské výšce. Čas by tak měl být to jediné, co je odděluje. Klimatické změny se tak mohou stát jedinou dominantní sledovanou proměnnou.

# 7 Poděkování

Tímto bych rád poděkoval všem, kteří byli nápomocni při realizaci tohoto výzkumu, zvláště pak spoluautorům všech předložených publikací. Mé vřelé poděkování rovněž patří pracovníkům paleontologického oddělení Národního muzea a zaměstnancům Severočeských dolů v Bílině, kteří mně nezištně zpřístupnili své paleontologické sbírky. Tento výzkum byl podpořen grantem GA ČR 14-23108S.

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## Článek I

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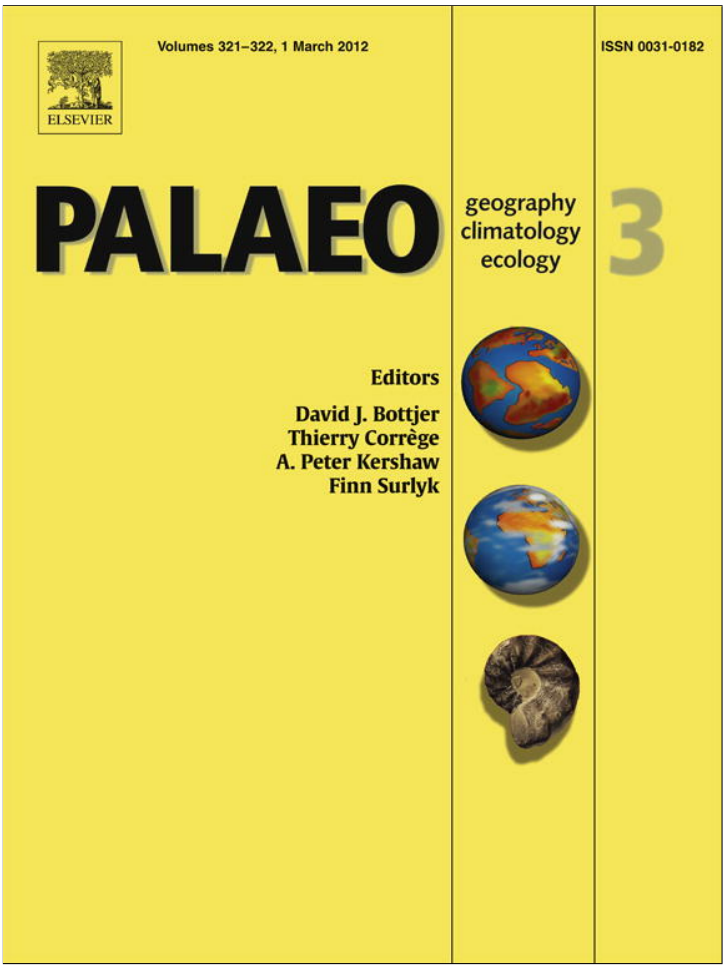

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# Plant–arthropod associations from the Early Miocene of the Most Basin in North Bohemia—Palaeoecological and palaeoclimatological implications

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ABSTRACT

Terrestrial plants and insects account for the majority of the Earth's biodiversity today, and herbivorous interactions are dated back more than 400 million yr. However, investigation of their associations remains in its infancy in Europe. The Miocene is characterized by palaeogeographic re-organization due to the collision of the African with the Eurasian plates. Antarctica's enormous impact on global climatic conditions, and thus on European palaeoenvironment, resulted from a series of episodes of minor glaciations in the Early Miocene after the initial cooling and ice sheet formed during the Oligocene.

More than 3500 plant remains showing various kinds of feeding damage were available for the present study. These trace fossils are classified according to their external morphology into damage types (DT) and grouped to functional feeding-groups. The Neogene plant record in Europe is rich and diverse, offering a profound large-scale understanding of the floristic and vegetational development. A database of fossil traces from the Most Basin was compiled and analyzed by various statistical methods in terms of the diversity and intensity of palaeoherbivory. The primary objective is to present results on the development of insect herbivory through the section of the Bílina Mine in North Bohemia, with the aim of understanding the principal factors that caused the observed phenomena. The research was focused on two horizons—Delta Sandy Horizon (DSH) and Lake Clayey Horizon (LCH)—both sufficiently represented to compare their palaeoecological and palaeoclimatological signals on the basis of the presence of damages caused by insects and other herbivorous arthropods. A total sample of 60 different damage types, attributed to eight main functional feeding groups, was examined. Results from analyses of the frequency and diversity of the selected categories of plant arthropod associations within both examined horizons significantly support different environmental conditions. The LCH seems to be affected by the relatively colder and drier climatic conditions as indicated by a four times greater frequency of leaves with galls and lower taxonomic diversity and species equability, whereas DSH indicates warmer and more humid conditions reflecting the higher diversity of the plant species and damage types.



## 1. Introduction

The ecology of plant–insect associations currently is a significant aspect of modern ecological research. Consequently, studies of insect herbivory on fossil leaves provide crucial information on the ecology of feeding associations and the association of plants and their insect herbivores that cannot otherwise be obtained separately from the record of plant macrofossils and insect body fossils. Because food webs incorporating plants and phytophagous insects account for up to 75% of global diversity, it is essential to examine how factors like global warming and cooling affect insect herbivory.

The Earth's climate was gradually cooling during the Tertiary (the last 65 Ma). This trend was punctuated by three more abrupt cooling steps (e.g., Zachos et al., 2001a). Palaeoclimate indicators suggest that the East Antarctica ice-sheet formation, which initiated in the Late Oligocene (Lyle et al., 2007), resulted in a decrease in global sea level by nearly 70 m during this time (Berggren et al., 1995; Berggren, 2002). Subsequently, in the Miocene important vegetation changes resulted from this altered global climate (Utescher et al., 2011, and references herein). These changes were mainly triggered by fluctuations in and later expansion of the Antarctic continental ice-sheet (Barker and Thomas, 2004; Shevenell et al., 2004). Except at the very beginning of the Early Miocene, the glaciation of Antarctica was ephemeral and unstable compared to the present extent (Naish et al., 2001) and the Northern Hemisphere was largely ice-free at that time (Billups, 2002, and references therein). The Early to Middle Miocene

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glaciation fluctuations, which were probably caused by Milankovitch cycles, came to an end with the final deep-freezing of Antarctica in the mid-Miocene (Zachos et al., 1997, 2001b; Shevenell et al., 2004). Constant decrease of $pCO_2$ is suspected to be one of the most probable causative factors (Holbourn et al., 2005). All of these events deeply affected terrestrial ecosystems, especially in mid latitudes (Casanovas-Vilar et al., 2005; Böhme et al., 2008; Wappler, 2010).

The study of plant–insect associations during the Early Miocene thus gives an opportunity to test some important predictions with regard to climatic fluctuations of the time. The European Miocene has not been subjected to such a detailed analysis of plant–insect associations and allows significant, new and extended understanding of Miocene regional climate dynamics and how they differ from those of the present day. A fossil assemblage covering this time period coupled with excellent preservation of insects and plants is the Early Miocene deposit at Bílina Mine. The Early Miocene Lagerstätte of Bílina Mine in the Most Basin, Czech Republic provides a unique view into a Neogene freshwater ecosystem and records a time of significant changes in climate, biodiversity, and floral and faunal composition (Kvaček et al., 2004).

Herein we document changes in insect herbivory through the Early Miocene, with the aim of understanding the principal factors involved in the observed variations, combined with a variety of proxies to estimate palaeotemperature, precipitation, and nutrient levels (e.g., Pearson and Palmer, 2000; Utescher et al., 2000, 2011; Mosbrugger et al., 2005; Uhl et al., 2006, 2007).

## 2. Materials and methods

The material studied is housed in the National Museum in Prague, the Bílina Mine Enterprise collections, and the Senckenberg Naturhistorische Sammlungen Dresden. The Bílina Mine collection comprises material from 23 fossiliferous layers belonging to three different horizons [Clayey Superseam Horizon (CSH), Delta Sandy Horizon (DSH), Lake Clayey Horizon (LCH) *sensu* Bůžek et al. (1992), see Fig. 1] (see also supplementary material in Appendix 2). The collection from the Břešťany locality consists entirely of the specimens found in Břešťany clayes stratigraphically identical with LCH of the Bílina mine. Both localities are situated in the Most Basin and belong to the Most Formation of Early Miocene age. The sedimentation of Most Formation represents coal-bearing basin fill that can be divided into four basic units: Duchcov ("Underlying"), Holešice ("Main Seam"), Libkovice ("Overlying") and Lom ("Lom Seam") members *sensu* Domácí (1977). The deposits of CSH and DSH consisting of sandy–clayey delta bodies and overlying the main lignite seam are included into the Holešice Member, the LCH deposits are situated at the lowest part of Libkovice Member. Accurate setting of geological age and stratigraphical extend of individual units is unavailable due to the lack of volcanic rocks allowing radioisotope dating. Nevertheless, the rocks underlying the main coal seam of Holešice Member were dated to mammal zone MN3 of Early Burdigalian (~Early Eggenburgian) age—see Fejfar (1989), Fejfar and Kvaček (1993). The Libkovice Member of the Most Basin has been dated by palaeomagnetic study (Bucha et al., 1987). For the lower part of this member, comprising the Břešťany clayes the age of 20 Ma was given. According to the different floral assemblages occurring in specific sedimentary environments, all three horizons represent distinct ecosystems: 1) swamp forest, 2) riparian–levee forest and 3) upland lakeshore forest (Bůžek et al., 1987; Boulter et al., 1993; Kvaček et al., 2004). However, various types of the forest vegetation give only approximate palaeoclimatic data and the ratio of deciduous *vs.* evergreen woody elements does not indicate very precisely the variation of the palaeoclimatic conditions. The palaeoclimatic estimation using CLAMP method was made only for the Břešťany flora and the following values were obtained (Teodoridis and Kvaček, 2006): Mean Annual Temperature (MAT) $15.9 \pm 1.2$ °C; mean temperature of the warmest month (WMMT) $25 \pm 1.6$ °C; mean temperature of the coldest month (CMMT) $7 \pm 1.9$ °C. The age and geological and palaeoclimatic setting of the Most Basin (in preceding literature so-called North Bohemian Brown Coal Basin) has been also briefly summarized by Kvaček (1998) and Prokop et al. (2010).

More than 4300 specimens of plant compression fossils have been examined, most of which are leaves of woody dicotyledonous plants (Table 1). Water plants and gymnosperms were excluded from the statistical analysis due to their rarity of affliction. The resulting 3509 specimens were examined for the presence of insect damage, which was determined to damage types according to Labandeira et al. (2007; and subsequent edition in prep.). Furthermore, the fossils

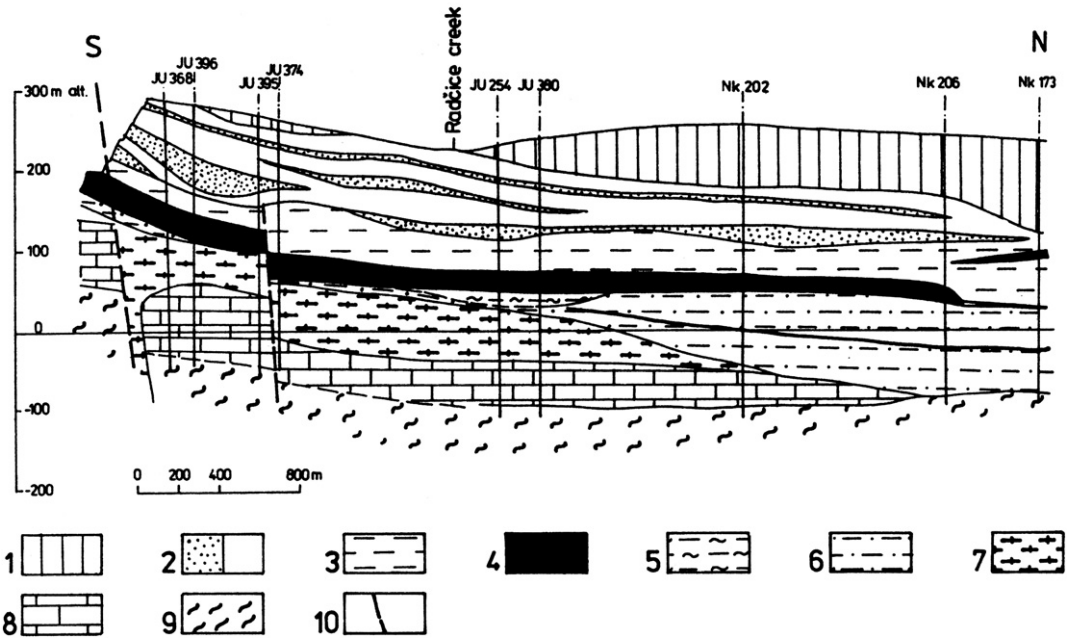



**Fig. 1.** Geological section of the Bílina Mine. (1) Lake Clayey Horizon; (2) Delta Sandy Horizon (sand, clay); (3) Clayey Superseam Horizon; (4) Coal Seam; (5) coaly clay; (6) Lower Sandy–clayey Member; (7) Neovolcanites; (8) Upper Cretaceous; (9) crystalline basement; (10) fault (adopted from Bůžek et al., 1992).

**Table 1**
Site summaries—fossiliferous horizons.

| Horizon | Age [Ma] (Kvaček et al., 2004) | MAT (°C) (Teodoridis, 2006) | Leaves in the census | Damaged leaves (only dicots) | | Damaged leaves (incl. monocots) |
|---|---|---|---|---|---|---|
| | | | | leaves | % Damage | |
| DSH | 20.8–18.3 | 16.5 ± 1.7 | 2233 | 571 | 25.6 ± 0.92 | 745 |
| LCH | 20.8–18.3 | 16.5 ± 1.7 | 1260 | 220 | 17.5 ± 1.07 | 257 |
| CSH | 20.8–18.3 | 16.5 ± 1.7 | 16 | 9 | 56.3 ± 12.4[a] | 13 |

[a] In this case, standard deviation is so high because of the low number of available specimens.

leaves were evaluated according to the following aspects: (1) the taxonomic attribution, (2) the stratigraphic position, (3) leaf economics (*sensu* Royer et al., 2007), and (4) their classification to one of the three mentioned horizons. These damage types (DTs) can be classified further into eight functional feeding groups (FFG): hole feeding (HF), margin feeding (MF), skeletonization (S), surface feeding (SF), galling (G), mining (M), piercing and sucking (PS), and oviposition (O) as described elsewhere (Labandeira et al., 2002, 2007).

Quantitative analysis of insect damage occurrence and diversity was done in the R 2.10.0 statistical environment (R Development Core Team, 2009). The differences among the proportions of occurrence of individual functional feeding groups (FFG) were analyzed by $\chi^2$ test. The remaining analyses were done by using the generalized linear models (GLM) of the binomial family. The percentage of explained variability was computed by means of Nagelkerke pseudo-$R^2$ measure as implemented in the Design 2.3-0 R-package (Nagelkerke, 1991; Harrell, 2009). Where necessary, over dispersion was treated by refitting to quasibinomial family of GLM and subsequent use of *F* tests at appropriate places (Crawley, 2007).

A generally more crucial issue was how to obtain comparable samples from the two horizons, both having sufficient input data for statistical analysis (Clayey Superseam Horizon [CSH] was too small to be analyzed statistically). This is especially important for comparing the sample diversities. A usually adopted approach is that of rarefaction curves (often following Tipper, 1979). However this approach cannot be employed for the compression fossil data, since each leaf bears zero to several damage types caused by insects, therefore a sample-based rarefaction curve should be applied (according to terminology by Gotelli and Colwell, 2001). Moreover the rarefaction curves constructed by resampling the assemblage without replacement produce correct estimates of species richness, but the standard errors of the estimate are generally smaller, depending on the ratio of the size of subsample to the original size of the assemblage. An alternative is to construct rarefaction curves by sampling with replacement, in which case we obtain underestimated species richness but unaffected standard errors (Colwell, 2009). This method is therefore "a better evil", if we aim to test statistically the differences in species richness among rarefied subsamples from different assemblages.

Therefore we constructed the rarefaction curves in our study by means of resampling with replacement. The same procedure was also used for construction of samples for statistical testing. We drew randomly such sizes and such numbers of replicates so that the total number of drawn specimens was smaller or equal to the total number of specimens in the appropriate assemblage. This was adopted in order to avoid pseudoreplication.

In order to separate the causes of changing interactions into plant composition component and climate, we used two types of datasets. The first were the complete assemblages of dicotyledonous plants from the DSH and LCH horizons. The second dataset was the subset of 8 species, which occurred in both horizons and were represented by more than 25 specimens in each.

Every fossil leaf that clearly shows the attachment of a complete petiole to the blade and had a reconstructable leaf area was used in a leaf mass per area ($M_A$) analysis. The $M_A$ analysis uses the robust global correlation in extant leaves of petiole width squared and leaf mass, both normalized for leaf area, to estimate leaf mass per area in fossils (Royer et al., 2007). For this purpose only those specimens were used, for which both margins of the petiole are preserved and for which leaf area could be reasonably estimated by digital reconstruction and measurement of photos. Measurements were made using Image J (http://rsb.info.nih.gov/ij), and $M_A$ values were calculated using the protocol of Royer et al. (2007).

## 3. Results

### 3.1. Fossil assemblages of plant–insect interactions within the horizons

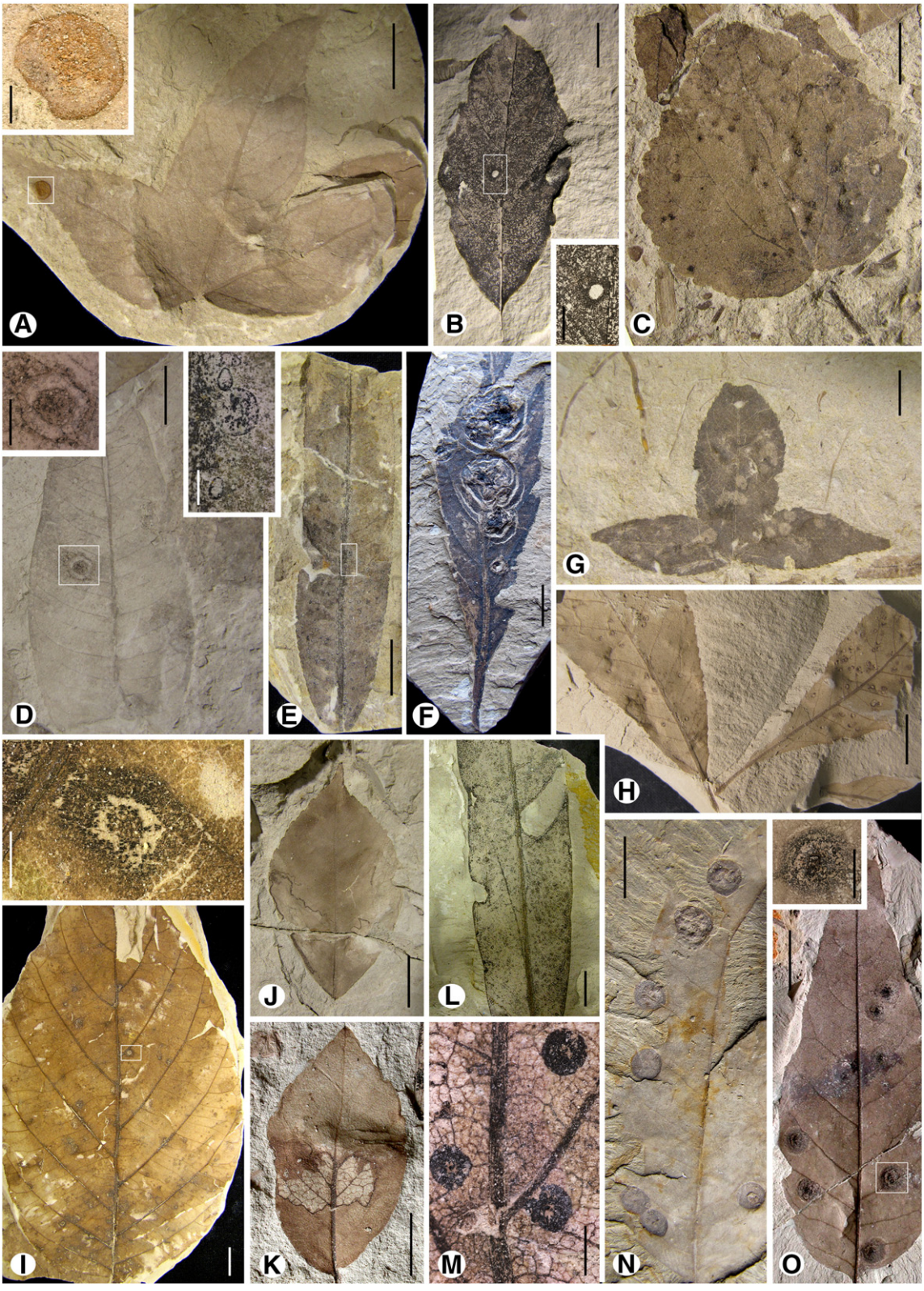
Of the examined 3509 fossil specimens, 727 bore at least one damage type (see Fig. 2A–O). Altogether, 60 different damage types were recorded.

#### 3.1.1. Delta Sandy Horizon—DSH

Of the 2233 dicotyledonous leaves from the DSH, 2215 were identified to 80 plant species within 28 families (see also supplementary material in Appendix 1, Table S1). 571 specimens (25.6%) have some type of damage and so they show the presence of at least one functional feeding group. The occurrence of the damage is recorded in 745 cases, representing 54 different types. The majority of damaged specimens show evidence of hole feeding with 356 occurrences, followed by margin feeding with 230 occurrences. Skeletonization and galling are recorded with almost the same frequency, with 63 and 61 occurrences, respectively. Galling shows the presence of 13 distinct types of damage. Mining is present in 23 cases represented by 11 different types. The lowest frequency (9) can be found in the case of surface feeding. There was no evidence of piercing and sucking. The group of specialized damage types has relatively little abundance of occurrences (106), but relatively high diversity (33 different types). Most of the damaged leaves (73.9%) bear only a single type of damage, followed by 22.5% damaged leaves with two types of damage, 2.6% of damaged leaves occurred with three types and only

**Fig. 2.** Representative insect plant interactions of the Most Basin flora. (A) Blotch mine without central chamber on *Liquidambar europea* (Hamamelidaceae) with enlarged view of mine in upper left corner (DB5_180, DT36); (B) Circular gall, lacking central tissue, surrounded by the rim of thick tissue on *Alnus julianiformis* (Betulaceae) with enlarged view of gall in bottom right corner (DB3_255, DT11); (C) Circular galls on *Cercidiphyllum crenatum* (Cercidiphyllaceae) (DB48_157, DT11); (D) Circular gall with large fusanized core separated from thinner outer rim on *Decodon gibbosus* (Lythraceae) with enlarged view of gall in upper left corner (DB2_111, DT49); (E) Probable damselfy oviposition along midrib on *Salix haidingeri* (Salicaceae) with enlarged view in upper left corner (DB21_250, DT76); (F) Large galls on *Quercus rhenana* (Fagaceae) (G_7647, DT84); (G), Circular mining on *Liquidambar europea* (Hamamelidaceae) (DB24_187, DT38); (H) Dispersed galls on *Carya* sp. (Juglandaceae) (DB57_379, DT163); (I) Blotch mine on *Alnus julianiformis* (Betulaceae) with enlarged view of mine above. (DB36_216, DT36); (J) Stigmella-type mine on ?*Schisandra* (Schisandraceae) (DB36_186, DT41); (K) Skeletonization with poorly developed reaction rim on *Viburnum atlanticum* (familia incertae sedis) (ZDI041, DT16); (L) Dispersed marginal feeding on *Quercus rhenana* (Fagaceae) (DB24_153, DT1, 12, 14); (M) Circular solid galls of uncertain origin with central canaliculus on an unidentifiable dicot (DB71_158); (N) Circular impressions of probably piercing–sucking scale armoured insect (Hemiptera: Coccoidea) on *Leguminosites* sp. (Fabaceae) (G_7627, DT53); (O) Spheroidal galls with central chamber surrounded by thick wall and second tissue layer on *Fraxinus bilinica* (Oleaceae) with enlarged view of gall in upper left corner (ZDI023, DT145). A–F, H–J, L, N, O—scale bar represents 10 mm; K—5 mm; M—1 mm. Enlarged areas: A, E, I—scale bar represents 1 mm; B, D, O—3 mm.

0.9% of damaged leaves exhibit four types. The five most abundant host plant taxa, accounting for one-quarter of the fossil leaves in the DSH, are affected by more than 30.6% of insect damage occurrences documented therein (Fig. 3A). *Alnus julianiformis* is the most abundant taxon (7.4%) in the DSH and is also one of the most consumed species (31.9%). The corresponding diversity of 19 different types of damage is the highest in the whole assemblage. Second in order of most numerous taxa, *Ulmus pyramidalis* (5.3%) represents a considerably lower proportion of damaged leaves (14.4%) and absolute diversity of types of damage. Three other similarly numerous taxa—*Acer tricuspidatum* (4.1%), *Nyssa Haidingeri* (3.9%), and *Alnus gaudini* (3.8%) exhibit a similar proportion of damaged leaves (27.5%, 20.7%, and 28.2%). *Populus zaddachii* var. *brabenecii* has the highest level of damage (56.8%) among the taxa that count 25 and more specimens



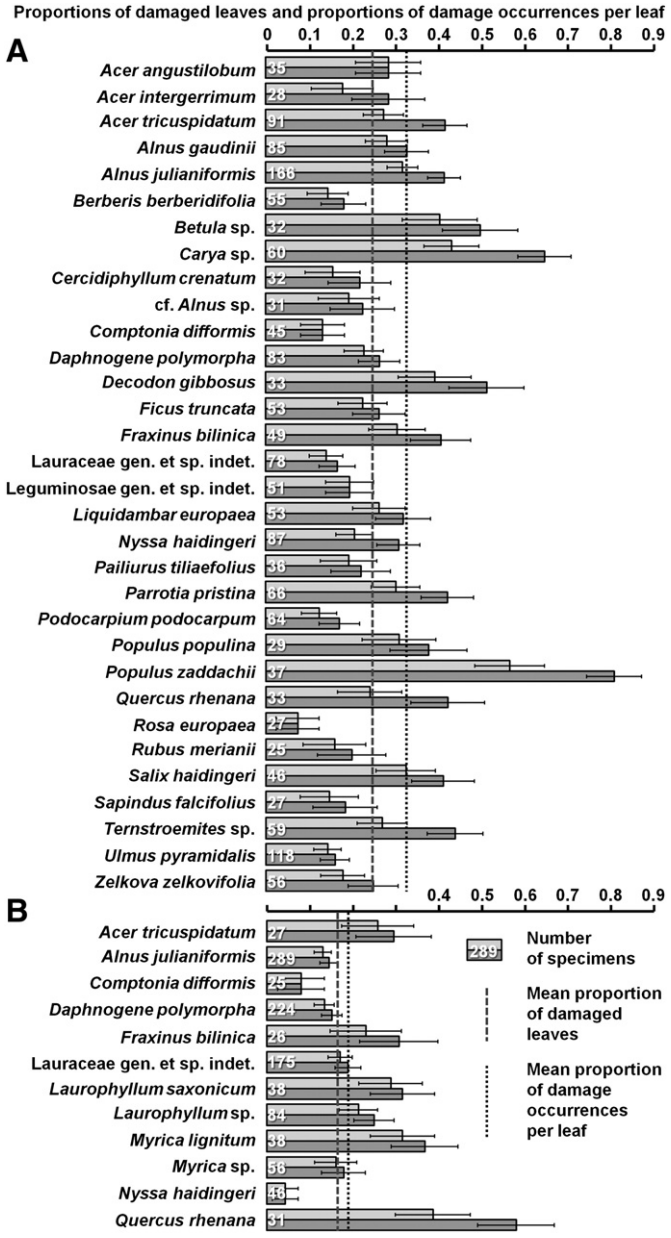



**Fig. 3.** Percentage of leaves exhibiting feeding traces and percentage of damage occurrences per one leaf from the most abundant genera ($N \geq 25$ specimens). (A) DSH assemblage, (B) LCH assemblage. Light grey bars representing percentage of damaged leaves, dark grey bars the damage occurrences per one leaf. Error bars show standard deviation for the selected taxa.

occurring at both horizons. Both *Betula* sp. and *Decodon gibbosus* show almost the same proportion of damaged leaves (40.6% and 39.4%) and the diversity of damage types (7 and 9, respectively.). On the other hand, *Rosa europaea* (37 specimens), with only 7.4% damaged leaves, exhibits also a low diversity of only two damage types (DTs 3, 8). The fairly abundant (45 specimens) *Comptonia difformis*, with 13.3% of leaves damaged, surprisingly has the lowest diversity of types of damage, with only a single type of damage (DT 12).

#### 3.1.2. Lake Clayey Horizon—LCH

In total 1260 dicotyledonous specimens in the LCH were recorded. They could be classified into 46 separate taxonomic entities belonging to the 13 families (see also supplementary material in Appendix 1, Table S2). 220 specimens (17.5%) have some indication of damage, representing in total 33 different types. The functional feeding groups are mostly represented by galling and marginal feeding. Both show the same frequency in the LCH of 88 occurrences. Most of the damaged leaves (85.5%) bear only a single type of damage, followed by 12.3% damaged leaves with two types, and only 2.3% of damaged leaves occurred with three types. The most palatable taxon is *Alnus julianiformis* (family Betulaceae), accounting for 23% of all herbiverous insect attacks and the greatest diversity of damage types (11 DTs), followed by three numerous taxa from the Lauraceae—*Daphnogene polymorpha* (17.8%, 7 DTs), Lauraceae gen. et sp. indet., and *Laurophyllum* sp. Evergreen bog oak, *Quercus rhenana* (Fagaceae), and *Myrica* sp., both have the highest percentage of damaged leaves from the sample with at least 25 specimens having 38.7%, and 31.6%, respectively, of damaged leaves. They are followed by *Laurophyllum saxonicum* with 28.9% damaged leaves. The occurrence of the highest level of damage of species with more than 10 fossil specimens can be observed in *Laurophyllum pseudoprinceps* (42.8%). Among the numerous plant species, *Nyssa haidingeri*, with two types, exhibits the lowest level of damage diversity with only 4.3% of damaged leaves and a low level of frequency of damaged leaves (Fig. 3B).

### 3.2. Comparison of the diversity of plant taxa

Both horizons are significantly different not only according to their diversity of plant taxa, but also in the proportional representation of plant species. LCH appears to be significantly poorer in taxonomic diversity, with 46 different taxa of different taxonomic levels, compared with 81 in the DSH. Therefore both sets include a different number of fossil leaves; the sample size for each horizon was standardized by the aforementioned modified rarefaction methods. Results from accumulation curves (Fig. 4A–C) were derived from three different datasets from both horizons according to the level of taxonomic determination. The first included all taxa listed in Tables 1 and 2, (inclusive of dicot. indet.). The second eliminated all taxa above species and incompletely identified types (sp. cf., sp. div., sp.). The same procedure was finally applied to all known genera. All three differences in plant diversity between horizons were statistically significant ($p<0.001$, tested on the basis of binomial generalized linear family model), so the initial assumption of greater diversity of plant taxa in the DSH was confirmed.

### 3.3. Comparison of DSH and LCH damage levels

#### 3.3.1. Functional Feeding Groups (FFG)

Based on the results of chi-square test ($\chi^2 = 111.14$, $df = 5$, $p<0.001$), it can be concluded that each category of functional feeding groups differs significantly between the horizons. Similar proportions, but of distinct FFG can be seen in the case of taxa with an occurrence of $\geq 25$ specimens in both horizons. Another significant difference is the occurrence of skeletonization, which in the DSH is nearly one-half the relative frequency of that of the LCH. The relative incidence of mining in the DSH is about 50% higher than in the LCH. Galling constitutes one-third of the total diagnosed damage in the LCH, which is more than four times in the DSH. Otherwise, the DSH exhibits significantly higher values of damaged leaves than the LCH. 531 (25.6%) of the total of 2233 leaves in the DSH have some type of damage, compared to 220 (17.5%) of 1260 leaves documented from the LCH. The total number of 745 instances of damage in the DSH represents an average of 0.33 different types of damage per fossil leaf, while the total number of 257 instances of damage in LCH represents only 0.20 of distinct damage type occurrence per fossil leaf in the whole dataset. Differences between horizons in terms of ***(1)*** the total percentage of damaged leaves and ***(2)*** the number of different types of leaf damage per one leaf is confirmed by the results of statistical tests. The difference in the proportion of damaged leaves was tested between the horizons by chi-square test ($\chi^2 = 29.79$, $df = 1$, $p<0.001$) and the difference concerning the number of distinct

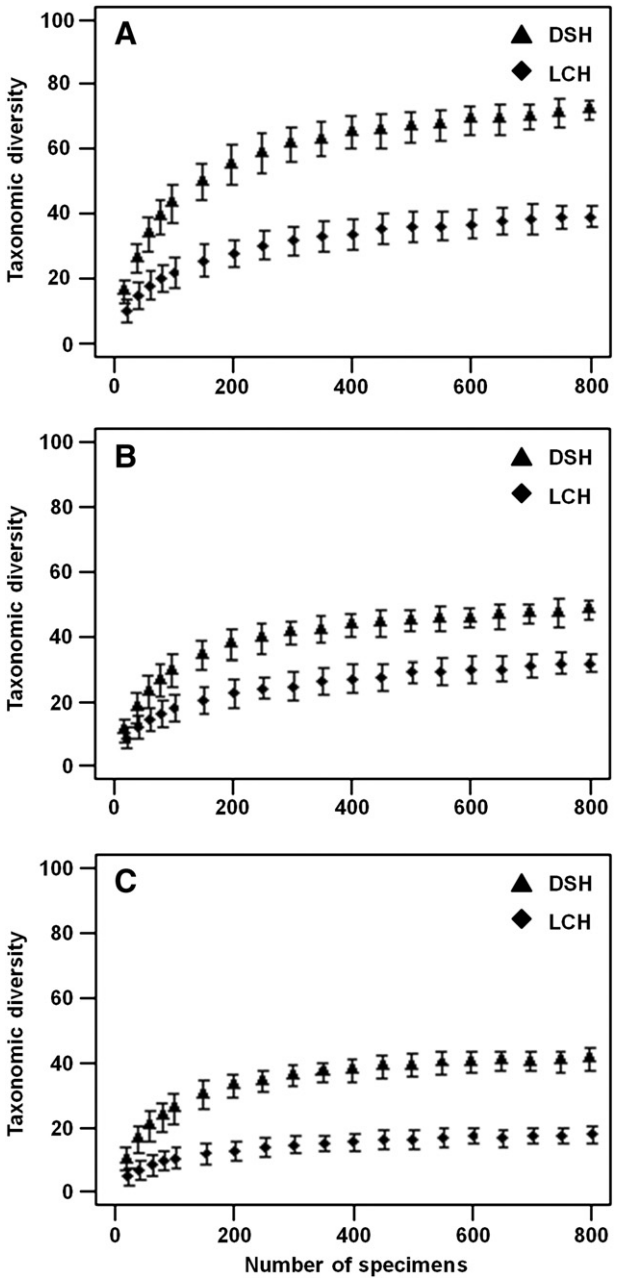



**Fig. 4.** Plant taxonomical diversity. (A) Dataset with all taxa. (B) Dataset with undoubtedly identified species. (C) Dataset with undoubtedly identified genera. Error bars indicate standard error of the mean.

damages per one leaf were also tested by chi-square test ($\chi^2 = 13.40$, $df = 3$, $p = 0.004$). Both sets were also tested for differences in the types of damage within each functional feeding group (Fig. 5).

Oviposition and piercing and sucking were excluded owing to insignificant frequencies. Based on the five chi-square tests for each

**Table 2**
Differences for recognized functional feeding groups (FFG's) between horizons.

| Responsible variable | DSH | LCH | $\chi^2$ | *df* | *p*-Value |
|---|---|---|---|---|---|
| Hole feeding | 14.6% | 4.5% | 82.73 | 1 | <0.001 |
| Marginal feeding | 9.3% | 6.8% | 5.95 | 1 | 0.015 |
| Skeletonization | 2.8% | 0.7% | 16.69 | 1 | <0.001 |
| Surface feeding | 0.4% | 0.1% | 1.93 | 1 | n.s. |
| Galling | 2.7% | 6.6% | 29.33 | 1 | <0.001 |
| Mining | 1.0% | 0.5% | 2.37 | 1 | n.s. |

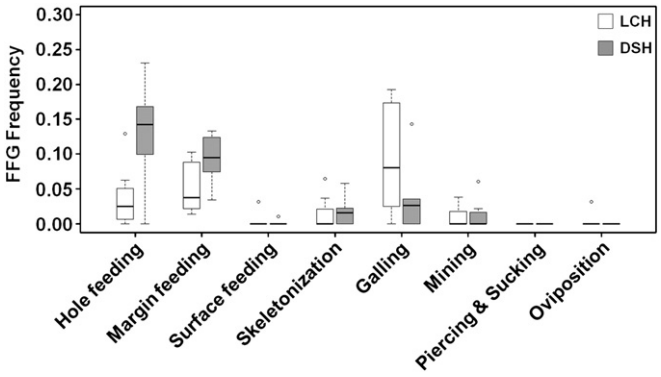



**Fig. 5.** Box plots of FFG frequency for the eight most abundant taxa (≥25 specimens) occurring in both horizons.

functional feeding group it can be concluded that the percentage of leaves affected by damage belonging to the same functional feeding group between horizons are different in all cases except mining and surface feeding (see Table 2).

*3.3.2. Comparison between the diversity of FFG and DT*

The results confirm differences in the degree of damage type diversity, as well as a slight difference in the diversity of the functional feeding groups rarified to 100 fossil specimens (Fig. 6). Measures of diversity rarified to 100 fossil specimens between the two horizons differ significantly in the case of diversity of (1) all types of damage, and (2) represented functional feeding groups ($p<0.001$ and $p=0.024$, respectively, see Table 3). Testing for possible causal relationships between insect herbivores, host plants, plant autecology and taxonomic diversity is somewhat more complicated. Particularly, variations in herbivore composition through time illustrate changes in the importance of different damage types or functional feeding groups across the abundant plant species from the two horizons (Fig. 7A–E). After correction of the differences between the horizons for the differences in plant species composition and the variability of the diversity observed among categories of damage, significant differences of diversity were found in the case of (1) all types of damage, (2) specialized damage, and (3) formation of galls (see Table 3). The properties of horizons themselves have a more conspicuous impact, particularly on diversity of all types of damage (15.5% explained variation). However, it can be noticed that the autecology of each species affects the degree of diversity of the categories of damage types rather more than ecological conditions characterized by the horizons as evidenced by a significantly higher amount of variability explained by the factor of taxonomic affiliation (between 40% and 55% compared with up to 15% explained by horizon affiliation). The diversity of specialized damage, galls and mines, sampled to the size of 100 rarified fossils, shows no significant differences between the horizons. We also used binomial linear models for analysis, which served as input data the average rate of eight pairs of the diversity of the taxa from five repeated iteration cycles of 25 fossils for each combination of predictors (species or horizons) and the identity of the species inserted into the model to position of the covariates (i.e., the factor term of the model equation).

In terms of insect taxonomic diversity it is important to establish the diversity of all damage types and some selected functional feeding groups, such as specialized types and galls rarified to the number of their occurrences in the same category. The shape of the resulting accumulation curves is rather different (see Fig. 8A–C) from the accumulation curves generated to the diversity of the damage types rarified to the number of fossil leaves. The accumulation curves and the tested average values of the diversity of damage types or functional feeding groups introduced here were obtained by re-sampling with

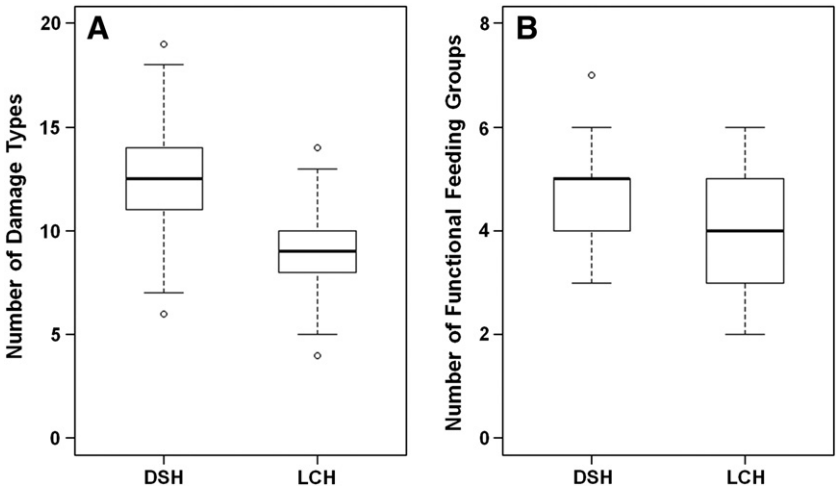



**Fig. 6.** Mean diversity of damage type and functional feeding groups. (A) Mean diversity of damage type rarified to 100 leaves. (B) Mean diversity of functional feeding groups rarified to 100 leaves.

replacement. The input data were the whole data set for each of the two horizons and processed as before, using linear binomial models and the average diversity rate for all categories of observed types of damage, i.e. all types of specialized types of galls, rarified to 20 occurrences in five iterations.

When testing the diversities of functional feeding groups, as input data their diversities rarified to 20 occurrences of all types of damage from five iterations were also used. Testing of the species composition impact and of the individual plant species autecology influence on diversity of selected categories of damage types and functional feeding groups was also undertaken. As input data, the average levels of diversity of all the damage, the specialized types of damage, galling or functional feeding groups, rarified to five occurrences of the same category of damage from five iteration cycles, were used. Mining was excluded from the statistical processing due to its low number of occurrences in both horizons. Diversities were rarified to 20 occurrences of the respective types of damage between the two horizons as a whole and to five occurrences of the corresponding types of damage in case of the horizons represented by taxa documented by 25 specimens and more (after correction for the species composition and subsequently for the impact on taxa variability) were significant in specialized damage types. However, in this case, the influence of horizon itself on the variability of the diversity was small and the autecology of taxa played a substantial role (see Table 4).

### 3.3.3. Damage frequency vs. $M_A$

Total $M_A$ data were obtained from 11 species represented by 78 fossil leaves of the LCH and from 29 species represented by 152 fossil leaves of the DSH (see Table S8). The mean $M_A$ of leaves from the LCH is 96 $gm^{-2}$ with a confidence interval ranging from 106 to 87 $gm^{-2}$ and the average $M_A$ of leaves from the DSH is 85 $gm^{-2}$ with a confidence interval ranging from 92 to 77 $gm^{-2}$. The input data served for testing the correlation of (1) the proportion of leaves affected by different types of damage belonging to different functional feeding groups at the $M_A$, and (2) the dependence of the horizon, were used for the appropriate data from a number of 25 specimens and more.

Based on the results of these tests it can be proposed that the influence of $M_A$ on the FFG frequency is significant for hole feeding only, and the proportion of damaged leaves declines with rising $M_A$ in the DSH. On the other hand, a statistically significant influence of the horizon environmental conditions on different FFGs frequency can be demonstrated (Table 5, see also supplementary material in Appendix 1, Table S8).

## 4. Discussion

Early Miocene is a period in the beginning of Neogene that played a crucial role in the formation of contemporary ecosystems. In particular, the climatic turnovers caused by mainly tectonic events and geomorphologic processes influenced the ecosystem stability and biome changes (Agustí and Moyà-Solà, 1990; Beu et al., 1997; Barnosky and Carrasco, 2002; Sun et al., 2004; Blisniuk et al., 2005; Lyle et al., 2007; Mulch et al., 2010). Zachos et al. (2001b) demonstrates rapid changes of the mean annual global temperature resulting from the curve ratios of oxygen isotopes ($\delta^{18}O$) reflecting the temperature curve of oceanic waters. Thus, the climatic oscillations in the Early Miocene frequently occurred within a relatively short time period. The same trend can be observed in case of the global $pCO_2$ fluctuations that are supposedly connected with the changing climatic conditions as well (see also Fig. 8, Pagani et al., 2005). It could be expected that these relatively short-term climatic turnovers have detectable impacts on the Early Miocene ecosystems in the Most Basin. From the viewpoint of sedimentology our attention has been focused on the cumulative time span within the different horizons (DSH, LCH),

**Table 3**
Statistical significance of causal relationship of horizons environmental conditions, plants autoecology and the diversity level in case of diversity of different groups of damage rarified to the number of fossils.

| | Whole horizons | Taxa with at least 25 specimens in both horizons | | | |
|---|---|---|---|---|---|
| Type of interaction | | Taxon | Horizon | Taxon | Horizon |
| All types of damage | $p<0.001$ | $p<0.001$ | $p<0.001$ | 41.0% | 15.5% |
| Functional feeding groups | $p=0.024$ | $p<0.001$ | n.s. | 40.9% | - |
| Specialized types of damage | n.s. | $p<0.001$ | $p=0.019$ | 55.1% | 5.6% |
| Galling | n.s. | $p<0.001$ | $p=0.013$ | 53.5% | 6.7% |
| Mining | n.s. | $p<0.001$ | n.s. | 51.1% | - |

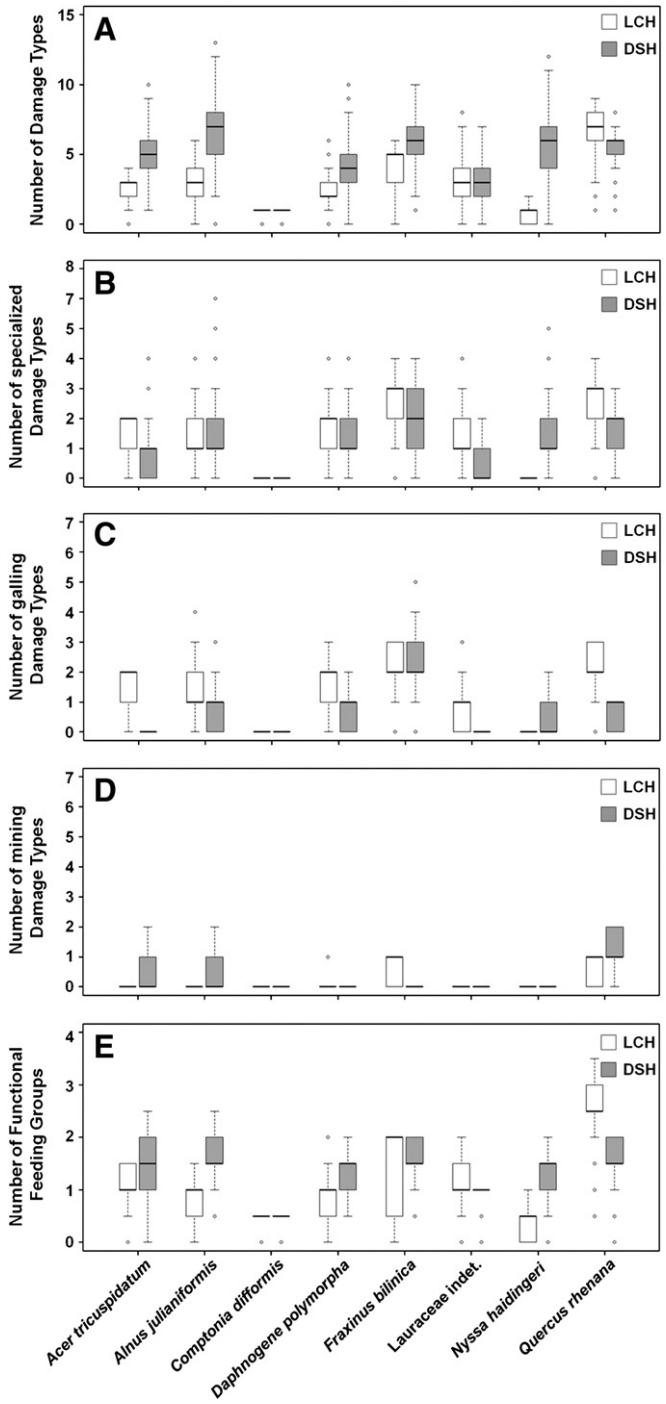



**Fig. 7.** Box plots of DT diversity for eight most abundant taxa (≥25 specimens) occurring in both horizons. (A) All types of damage. (B) Specialized types of damage. (C) Galling. (D) Mining. (E) Functional feeding groups.

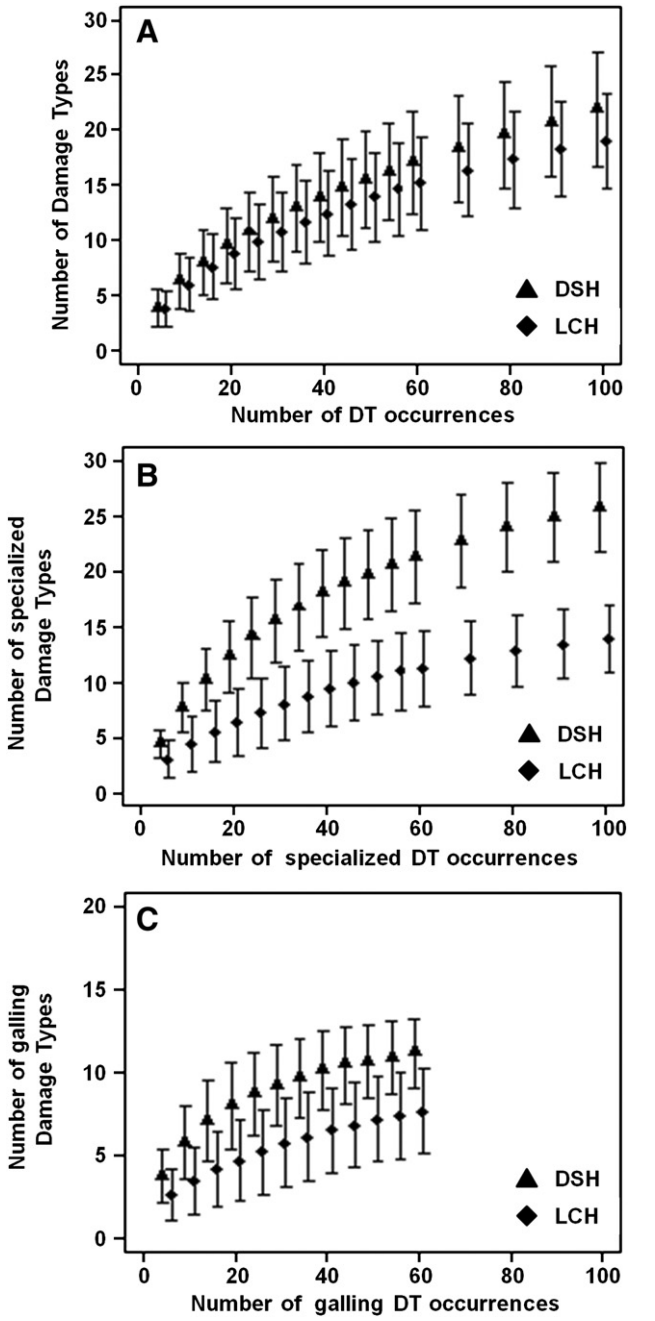



**Fig. 8.** Resampling curves—diversity of DT rarified to their own occurrence.(A) All damage types. (B) Specialized types. (C) Galling. Error bars indicate standard error of the mean.

which are represented by the distinct floral assemblages (Bůžek et al., 1992; Kvaček, 2000; Kvaček et al., 2004). Our effort was focused on the available palaeoclimate proxies presented by the level of insect caused leave damage. Kvaček (2000) attempted to separate the palaeoclimatical from other palaeoenvironmental factors, without giving a clear answer. Therefore, we analyzed only those characteristics of plant–insect interactions, which can be suspected to be affected by climatic conditions, i.e. ***(1)*** plant taxa diversity; ***(2)*** FFG and DT frequency; ***(3)*** FFG and DT diversity, and additionally; ***(4)*** influence of $M_A$ on FFG frequency (cf. Wilf, 2008).

### 4.1. Plant diversity and taxonomic composition

The Delta Sandy Horizon (DSH) has a greater taxonomic diversity of plants both in species richness and species equitability (more equal proportions of individual species). Given that the DSH horizon has a greater diversity and abundance of thermophilous elements, indicates a warmer and probably wetter climate (or rather with evenly distributed rainfall over time) than the LCH. The test of taxonomic equilibrium of both horizons indicates that both were well balanced, although there were several dominant taxa in the LCH. These results seem to be consistent with the previously published results of palaeofloristic research dealing with plant taxonomic composition of these two horizons after Kvaček and Teodoridis (2007), although some fluctuating differences occurred on various datasets used (see

**Table 4**
Statistical significance of causal relationship of horizons environmental conditions, plants autoecology and the diversity level in case of diversity of different groups of damage rarified to number their own occurrence.

| | Whole horizons | Taxa with at least 25 specimens in both horizons | | | |
|---|---|---|---|---|---|
| Type of interaction | | Taxon | Horizon | Taxon | Horizon |
| All types of damage | n.s. | 0.001 | n.s. | 58.5% | – |
| FFGs | n.s. | 0.005 | n.s. | 52.1% | – |
| Specialized types of damage | 0.005 | <0.001 | 0.024 | 54.6% | 8.3% |
| Galling | n.s. | <0.001 | n.s. | 53.7% | – |

Fig. 3a–c). The taxonomic composition is related to higher average values of proportion of evergreen xerophilous trees. This ecosystem experienced long dry periods, and drought deciduous, but $M_A$ is relatively high (Prior et al., 2003). Our results are consistent with the interpretation that the climate during LCH time was drier than or had a more uneven distribution of rainfall per year than DSH time.

### 4.2. DT and FFG frequency

Our results confirm the differences in the following parameters between the DSH and LCH horizons: (1) in the proportions of different functional feeding groups within each of the horizons and (2) the ratio among the respective functional feeding groups between these horizons. The relative differences between mutually relevant functional feeding groups belong to different horizons. The number of occurrences of galling is four times higher in the LCH compared to the DSH. This suggests a drier climate in accordance with the expectations based on other studies (Godfray, 1994; Price et al., 1998). Galling is the most represented functional feeding group for these taxa within the LCH, found mainly on leaves of *Acer tricuspidatum*, *Fraxinus bilinica*, and *Quercus rhenana*, with a frequency that meets or even exceeds the average rate of damaged leaves, while the marginal feeding, equally numerous in incidence in the LCH, is comparatively less on the leaves of these species. A higher proportion of damaged leaves and a relatively higher number of leaves with the presence of more different DTs in the DSH may be associated with a higher taxonomic diversity. It probably reflects favorable climatic conditions connected with higher population densities of insect herbivores (Coley and Aide, 1991; Coley and Barone, 1996; Wilf and Labandeira, 1999)

### 4.3. DT and FFG diversity

Comparison of DT and FFG diversity had to be resolved by two different approaches. The first was focused on the differences between the whole assemblages of all taxa, the second on selected taxa with occurrence of 25 or more in both horizons simultaneously. In the case of the horizons as a whole, significant difference in diversity was found only between the categories of all damage types and functional feeding groups. This is due to rarefaction to 100 specimens of fossil leaves. Based on the accumulation curve it can be assumed that in the case of rarefaction to 400 fossil leaves the results obtained a significant difference in the diversity of specialized types of damage in favor of the DSH, as well as in the case of the difference in their diversity rarified to the number of 50 occurrences of the DTs from the same DT group. This corresponds to a different number of fossil leaves in both horizons, but in both cases much more than 100 specimens. On the contrary, the difference in the diversity of functional feeding groups, which was based on rarefaction to the same number of leaves, is in favor of the DSH. Nevertheless their overall diversity is higher in the LCH despite of the lower number of leaves. This is a result of a single occurrence of the piercing and sucking in this horizon. However, these possible artifacts might not be recognized on other leaves from other tracks of this functional feeding group. Differences in the diversity of functional feeding groups seem to be unconvincing and the horizons are in this respect more or less equivalent. Between the two horizons there is a statistically confirmed significant difference in the diversity of all DTs in accordance with the assumption that a higher taxonomic diversity of host plants implies a higher diversity of insect herbivores, and thus a higher diversity of DTs (Knops et al., 1999; Haddad et al., 2001; Hawkins and Porter, 2003; Dyer et al., 2007). When comparing the horizons represented only by selected taxa occurring in both horizons with a frequency of 25 or more fossils, the determining factor in the difference in the diversities of the selected groups of damage appears to be intraspecific variation in damage to the diversity of selected taxa. A minor influence of the horizon palaeoenvironmental conditions on the diversity can be found only in the case of all types of damage, and to a lesser extent in the case of the specialized types of damage and galling.

The diversity of damage types and functional feeding groups rarified to the number of occurrences of the damage provides another view of the tested differences. In this case, the result provides a significant difference only in the case of specialized types of damage in favor of the DSH; while in the case of the diversities of all other observed categories no difference was found. The reason for these different results compared to the previous rarefaction method is the fact that the rarefaction to the number of occurrences of damage eliminates the impact of differences in proportionality of damaged leaves and in frequency of leaves with more than one DT between both horizons. Rarefaction to the number of occurrences of damage rather reflects the true diversity of insect herbivores, while the rarefaction to the number of leaves largely reflects the environmental conditions of the site (in this case essentially population density of insect herbivores). Noteworthy in this context is that the average diversity of specialized types of damage in the LCH is almost one-half the amount occurring in the DSH, this kind of damage constitutes almost two-fifths of occurrences of all DTs. One explanation may be that the most specialized type of damage represents galling, with a relative frequency four times higher in the LCH than in the DSH. When comparing the difference in diversity between the horizons represented by selected taxa occurring in both horizons with a frequency of 25 or more fossils, such as the main factor of the different diversities of selected damage groups, appears to bear intraspecific variation in diversity of damage in the case of selected taxa. After elimination of this phenomenon, horizon itself has little influence in the case of specialized types of damage.

**Table 5**
Impact of $M_A$ on FFG frequency.

| Proportion of affected leaves/ functional feeding group | Influence significance | | Percentage of explained variability | |
|---|---|---|---|---|
| | $M_A$ | Horizon | $M_A$ effect | Horizon effect |
| Hole feeding | <0.001 | <0.001 | 17.2% | 25.7% |
| Marginal feeding | n.s. | 0.007 | – | 4.0% |
| Surface feeding | n.s. | n.s. | – | – |
| Skeletonization | n.s. | n.s. | – | – |
| Galling | n.s. | 0.001 | – | 20.2% |
| Piercing and sucking | n.s. | n.s. | – | – |
| Proportion of damaged leaves | n.s. | 0.012 | – | 2.1% |

The first reason of different results obtained by various rarefaction methods is the elimination of influence of a higher proportion of damaged leaves in the DSH by the rarefaction to the number of damage occurrences. The second reason is a higher incidence of different types of damage per one leaf in DSH.

### 4.4. $M_A$ influence on FFG frequency

The DSH does not show any statistically significant effect of $M_A$ on the frequency of each functional feeding group with the single exception of hole feeding. In this case, the frequency clearly declines with increasing $M_A$. The cause could be the resistance of this leaf morphotype, with a solid sheet of outer protective cuticle, against this type of insect herbivory (Royer et al., 2007). This ascertainment is also in agreement with the statements of some previous works (e.g., Lucas et al., 2000; Roth-Nebelsick et al., 2001; Poorter et al., 2004). The question remains, why a similar dependence is not confirmed in the case of surface feeding where we can expect a similar "modus operandi" of herbivorous agent? The reason is probably the same as in the case of hole feeding in the LCH, in that it occurs in lower relative and absolute frequency of FFG in both horizons. The fact that the value of the $M_A$ does not affect the frequency of galling, as might be expected, may have a relatively simple explanation. Higher $M_A$ and higher frequencies of galling have a common cause, consisting of the lower average atmospheric humidity (Price et al., 1998; Cuevas-Reyes et al., 2004). High frequency of galling is reported on taxa from the LCH with low and relatively high $M_A$ index.

## 5. Conclusions

A comparison of the two horizons confirmed the differences in the character of their respective habitats resulting from different climatic conditions. In comparison with the DSH, the LCH appears to be a drier habitat with unevenly distributed rainfall and with lower overall diversity of all types of damage. A significant difference in diversity of different DT groups, with the exception of specialized damage, was not confirmed. However, the frequency of galling in the LCH is much higher, suggesting drier conditions in this habitat. Diversity of damage types was also lower in the LCH, but the individual DTs were more abundant and more specialized damage types occurred indicating a generally less connected network of plant–insect interactions with a higher degree of specialization.

According to the initial assumptions, the positive correlation of the overall damage frequency with increasing taxonomic diversity of host plants was confirmed. Diversity is significantly higher in the DSH: ***(1)*** in the case of all types of damage rarified for the bulk horizon data sets, and ***(2)*** in the case of specialized damage types rarified to the number of single damage occurrences. After a comparison of the horizons based on the eight most abundant taxa, the results show interspecific variability among the taxa as the most significant factor for the varying levels of the damage diversity. The habitat conditions of the horizon itself seem to have less influence than the plants autecology. The situation is somewhat different in case of the horizons represented by all taxa (whole datasets), where stronger environmental impact on the damage level can be found.

Furthermore, the link between climate habitat characters was confirmed and documented by taxonomic composition of the host plants and their average $M_A$ together with frequency of distinct FFG, especially galling, occurrence of which is typical for drier climatic conditions.

Overall, in the context of insect herbivory interaction, there are two main differences between the two horizons: (1) in the case of damage frequency and the proportion of leaves affected by different types of FFGs (number of distinct DT per leaf), and (2) in the case of the diversity of selected groups of damage types. This applies especially to the results obtained by rarefaction to the number of fossil leaves.

Diversity of selected DTs rarified to the number of occurrences with the corresponding damage type was significantly different in the case of specialized types of damage. This applies to the horizons as a whole and even after the separation of the influence of plant species composition and influence by species autecology. The considerable variability is probably affected by individual plant taxa autecology (intraspecific variability in the observed diversity) rather than the environmental conditions reflecting both horizons.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.palaeo.2012.01.023.

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# Supplement – Článek I

# Plant-Arthropod associations from the Early Miocene of the Most Basin in North Bohemia – Palaeoecological and palaeoclimatological implications

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# APPENDIX 1

# ELECTRONIC SUPPLEMENTARY MATERIAL

**Table S1.** Insect and floral composition at the Delta Sandy Horizon (DSH); DT – damage type

**Table S2.** Insect and floral composition at the Lake Clayey Horizon (LCH); DT – damage type

**Table S3.** Insect and floral composition at the Clay Superseam Horizon (CSH); DT – damage type

**Table S4.** Proportionality of individual taxa with number of specimens ≥ 25 at the site, together with proportionality of the damaged leaves, diversity of all DTs and FFGs and the diversity per one leaf at these taxa.

**Table S5.** Specialized damage, Galling and Mining – their total diversity, number of occurrences and number of occurrences per one leaf at the taxa with 25 and more specimens.

**Table S6.** Mean diversities of selected categories of damage rarified to 25 leaves of each taxa.

**Table S7.** Mean diversities of selected categories of damage rarified to their 5 own occurrences at each taxa.

**Table S8.** Total number of leaves together with number of leaves affected by distinct FFGs and the mean LMA of the each taxa.

**Table S1.** Insect and floral composition at the Delta Sandy Horizon (DSH); DT – damage type

| Family rank | Taxon | Leaves | Damaged (%) | No. DT | DT occurrences |
|---|---|---|---|---|---|
| Anacardiaceae | *Rhus noeggerathii* | 1 | 100 | 1 | 78 |
| Aristolochiaceae | *Aristolochia* sp. | 2 | 50 | 2 | 2,3 |
| Berberidaceae | *Berberis berberidifolia* | 55 | 14.5 | 7 | 2,3,12,13,14,16,39 |
| | *Mahonia bilinica* | 1 | 0 | 0 | |
| Betulaceae | *Alnus gaudinii* | 85 | 28.2 | 13 | 1,2,3,12,14,16,20,33,57,85 90,145,153 |
| | *Alnus julianiformis* | 166 | 31.9 | 19 | 1,2,3,4,5,7,8,11,12,13,14,15,16, 33,36,57,105,110,143 |
| | cf. *Alnus* sp. | 31 | 6 | 19.4 | 1,2,3,4,5,16 |
| | *Alnus menzelli* | 15 | 20 | 3 | 1,3,62 |
| | *Betula* sp. | 32 | 40.6 | 7 | 1,2,3,11,12,14,16 |
| | *Carpinus grandis* | 15 | 33.3 | 4 | 2,11,12,15 |
| | *Carpinus* sp. | 13 | 23.1 | 3 | 1,2,12 |
| Celticidae | *Celtis japeti* | 3 | 33.3 | 2 | 2,12 |
| Cercidiphyllaceae | *Cercidiphyllum crenatum* | 32 | 15.6 | 5 | 2,3,11,12,33 |
| Ebenaceae | *Diospyros brachycepala* | 4 | 0 | 0 | |
| Fabaceae | Leguminosae gen. et sp. indet. | 51 | 19.6 | 6 | 1,2,3,12,14,25 |
| | *Leguminosites* sp. div. | 6 | 0 | 0 | |
| | *Podocarpium podocarpum* | 64 | 12.5 | 8 | 2,3,12,14,16,29,33,143 |
| | *Wisteria* aff. *fallax* | 13 | 7.7 | 1 | 3 |
| Fagaceae | *Quercus rhenana* | 33 | 24.2 | 8 | 1,2,5,12,14,32,41,171 |
| | *Trigonobalanopsis rhamnoides* | 1 | 100 | 1 | 12 |
| Hammamelidaceae | *Liquidambar europea* | 53 | 26.4 | 7 | 2,3,12,14,16,36,38 |
| | *Parrotia pristina* | 66 | 30.3 | 9 | 1,2,3,5,8,11,12,16,30 |
| Juglandaceae | *Carya* cf. *costata* | 23 | 56.5 | 9 | 1,2,3,12,16,17,32,36,37 |
| | *Carya serrifolia* | 1 | 0 | 0 | |
| | *Carya* sp. | 60 | 43.3 | 10 | 2,3,11,12,14,16,32,110,145,163 |
| | *Engelhardia orsbergensis* | 17 | 11.8 | 3 | 2,12,14 |
| | Juglandaceae gen. et sp. indet. | 3 | 66.7 | 2 | 2,16 |
| | *Juglans acuminata* | 19 | 26.3 | 4 | 5,12,16,32 |
| Lauraceae | *Daphnogene polymorpha* | 83 | 22.9 | 11 | 1,2,3,4,8,12,15,16,32,80,81 |
| | *Daphnogene* sp. | 7 | 28.6 | 2 | 2,12 |
| | Lauraceae gen. et. sp. indet. | 78 | 14.1 | 8 | 2,3,5,12,13,14,15,63 |
| | *Laurophyllum pseudoprinceps* | 11 | 36.4 | 3 | 2,12,16 |
| | *Laurophyllum saxonicum* | 3 | 0 | 0 | |
| | *Laurophyllum* sp. | 7 | 14.3 | 2 | 5,171 |
| Lythraceae | Decodon gibbosus | 33 | 39.4 | 9 | 2,5,12,14,16,31,33,49,110 |
| Magnoliaceae | *Magnolia* sp. | 23 | 26.1 | 3 | 4,12,14 |
| Myriaceae | *Camptonia difformis* | 45 | 13.3 | 1 | 12 |
| | *Myrica lignitum* | 18 | 27.8 | 3 | 2,11,34 |
| | *Myrica integerrima* | 7 | 28.6 | 1 | 12 |
| Nyssaceae | *Nyssa haidingeri* | 87 | 20.7 | 15 | 1,2,3,4,5,9,11,12,14,15,16,21, 24,34,78 |
| Nelumbonaceae | *Nelumbium* cf. *bruchii* | 1 | 0 | 0 | |
| Oleaceae | *Fraxinus bilinica* | 49 | 30.6 | 10 | 1,2,3,11,12,17,32,34,80,144 |
| Platanaceae | *Platanus neptuni* | 16 | 37.5 | 4 | 1,2,12,16 |
| Rhamnaceae | *Berchemia multinervis* | 20 | 30 | 6 | 2,12,13,15,16,143 |
| | *Paliurus tiliaefolius* | 36 | 19.4 | 4 | 1,2,3,12 |
| Rosaceae | *Cratageus* sp. | 7 | 0 | 0 | |
| | *Rosa europaea* | 27 | 7.4 | 2 | 3,8 |
| | *Rosaceae gen. et sp. indet* | 5 | 0 | 0 | |
| | *Rubus merianii* | 25 | 16 | 5 | 2,3,12,14,63 |
| | *Rubus vrsovicensis* | 3 | 100 | 2 | 3,4 |
| | *Sorbus* sp. | 1 | 0 | 0 | |
| Saliciaceae | *Populus populina* | 29 | 31 | 5 | 2,3,5,12,15 |
| | *Populus zaddachii* | 37 | 56.8 | 15 | 1,2,3,8,9,11,12,14,16 17,25,33,36,51,163 |
| | *Salix haidingeri* | 46 | 32.6 | 11 | 1,2,12,14,16,25,36,78,79,80 |
| | *Salix* sp. | 15 | 26.7 | 4 | 1,8,14,36 |
| | *Salix varians* | 7 | 14.3 | 1 | 16 |
| Sapindaceae | *Acer angustilobum* | 35 | 28.6 | 6 | 1,2,4,16,32,201 |
| | *Acer integerrimum* | 28 | 17.9 | 6 | 2,3,12,16,32,164 |
| | *Acer* sp. | 10 | 10 | 1 | 14 |
| | *Acer tricuspidatum* | 91 | 27.5 | 11 | 1,2,3,5,8,12,14,16,25,36,60 |
| | Sapindaceae gen. et sp. indet. | 15 | 33.3 | 5 | 2,3,17,41,143 |

| | | | | | |
|---|---|---|---|---|---|
| | *Sapindus falcifolius* | 27 | 14.8 | 4 | 3,5,12,16 |
| Simaroubaceae | *Ailanthus* sp. | 1 | 100 | 1 | 33 |
| Theaceae | *Gordonia* sp. | 2 | 0 | 0 | |
| | *Ternstroemites* sp. | 59 | 27.1 | 9 | 2,5,8,12,14,15,16,29,145 |
| | Theaceae gen. et.sp. indet. | 17 | 41.2 | 4 | 2,4,12,14 |
| Tiliaceae | *Dombeopsis lobata* | 14 | 21.4 | 3 | 2,5,16 |
| | *Tilia brabenecii* | 9 | 44.4 | 3 | 1,2,11 |
| Ulmaceae | *Ulmus pyramidalis* | 118 | 14.4 | 8 | 1,2,3,12,14,16,41,78 |
| | *Ulmus* sp. | 12 | 16.7 | 4 | 3,5,12,41 |
| | *Zelkova zelkovifolia* | 56 | 17.9 | 7 | 2,3,5,12,13,14,16 |
| Viscaceae | *Viscum* sp. | 2 | 0 | 0 | |
| Vitaceae | Cf. *Ampelopsis* sp. | 7 | 28.6 | 1 | 5 |
| | *Vitis stricta* | 8 | 75 | 5 | 2,3,4,12,14 |
| Familia incerta | Dicot. indet. | 18 | 94.4 | 10 | 2,3,5,8,9,12,14,32,36,78 |
| | *Dicotylophyllum* sp. div. | 15 | 26.7 | 3 | 3,8,34 |
| | *Diversiphyllum aesculapi* | 16 | 12.5 | 3 | 1,2,12 |
| | *Ficus truncata* | 53 | 22.6 | 5 | 2,3,5,12,32 |
| | *Phyllites kvacekii* | 14 | 14.3 | 2 | 12,32 |
| | *Phyllites nemejcii* | 1 | 100 | 1 | 3 |
| | *Pungiphyllum cruciatum* | 14 | 14.3 | 2 | 12,111 |
| **Total** | | **2233** | **25.57** | **54** | **1,2,3,4,5,7,8,9,11,12, 13,14,15,16,17,20,21 24,25,29,30,31,32,33 34,36,37,38,39,41,49 57,60,62,63,78,79,80 81,85,90,105,110,111, 143,144,145,153,163, 164,171,201** |

**Table S2.** Insect and floral composition at the Lake Clayey Horizon (LCH); DT – damage type

| Family rank | Taxon | Leaves | Damaged (%) | No. DT | DT occurrences |
|---|---|---|---|---|---|
| Berberidaceae | *Berberis berberidifolia* | 1 | 100 | 1 | 13 |
| Betulaceae | *Alnus gaudinii* | 7 | 14.3 | 1 | 41 |
| | *Alnus julianiformis* | 289 | 13.1 | 11 | 2,3,4,5,12,14,32,33,34,57,110 |
| | *Alnus* sp. | 13 | 7.7 | 1 | 2 |
| | cf. *Alnus* sp. | 2 | 100 | 3 | 2,5,14 |
| | *Betula* sp. | 2 | 50 | 1 | 13 |
| Ebenaceae | *Diospyros brachycepala* | 1 | 100 | 1 | 12 |
| Fabaceae | Leguminosae gen. et sp. indet. | 1 | 0 | 0 | |
| | *Leguminosites* sp.div. | 4 | 25 | 1 | 53 |
| | *Podocarpium podocarpum* | 1 | 0 | 0 | |
| | *Wisteria* aff. *fallax* | 1 | 100 | 1 | 5 |
| Fagaceae | *Quercus rhenana* | 31 | 38.7 | 9 | 2,12,17,33,76,84,90,201,215 |
| | *Trigobalanopsis rhamnoides* | 2 | 0 | 0 | |
| Juglandaceae | *Carya* sp. | 6 | 0 | 0 | |
| | *Engelhardia orsbergensis* | 4 | 0 | 0 | |
| | *Juglans acuminata* | 3 | 0 | 0 | |
| Lauraceae | *Daphnogene polymorpha* | 224 | 13.1 | 11 | 2,5,12,32,33,41,110 |
| | Lauraceae gen. et. sp. indet. | 175 | 17.1 | 10 | 1,2,3,12,14,15,16,32,33,49 |
| | *Laurophyllum pseudoprinceps* | 14 | 42.8 | 4 | 12,14,32,33 |
| | *Laurophyllum saxonicum* | 38 | 28.9 | 7 | 2,5,12,16,32,33,34 |
| | *Laurophyllum* sp. | 84 | 21.4 | 8 | 1,2,12,14,32,33,117,145 |
| Lythraceae | Decodon gibbosus | 6 | 33.3 | 2 | 12,14 |
| Magnoliaceae | *Magnolia* sp. | 1 | 0 | 0 | |
| Myriaceae | *Camptonia difformis* | 25 | 8 | 1 | 12 |
| | *Myrica banksiaefolia* | 6 | 33.3 | 2 | 12,14 |
| | *Myrica intergerrima* | 3 | 0 | 0 | |
| | *Myrica lignitum* | 38 | 31.6 | 8 | 2,3,8,11,12,14,41,89 |
| | *Myrica* sp. | 56 | 16.1 | 4 | 2,12,17,50 |
| Nelumbonaceae | *Nelumbium* cf. *bruchii* | 1 | 0 | 0 | |
| Nyssaceae | *Nyssa haidingeri* | 46 | 4.3 | 2 | 2,12 |
| Oleaceae | *Fraxinus bilinica* | 26 | 23.1 | 6 | 12,32,33,36,78,84 |
| | *Fraxinus* sp. | 3 | 0 | 0 | |
| Rhamnaceae | *Paliurus tiliaefolius* | 1 | 0 | 0 | |
| Saliciaceae | *Populus zaddachii* | 1 | 100 | 1 | 34 |
| Sapindaceae | *Acer integrilobum* | 1 | 0 | 0 | |
| | *Acer* sp. | 2 | 1 | 50 | 2 |
| | *Acer tricuspidatum* | 27 | 25.9 | 4 | 12,16,33,215 |
| Theaceae | Theaceae gen. et.sp. indet. | 16 | 25 | 2 | 12 |
| Tiliaceae | *Dombeopsis lobata* | 6 | 0 | 0 | |
| Ulmaceae | *Ulmus pyramidalis* | 17 | 17.6 | 2 | 12,32 |
| | *Ulmus* sp. | 14 | 21.4 | 2 | 2,12 |
| | *Zelkova zelkovifolia* | 12 | 0 | 0 | |
| Vitaceae | *Vitis stricta* | 3 | 33.3 | 1 | 12 |
| Familia incerta | Dicot. indet. | 34 | 20.6 | 8 | 1,2,3,12,15,16,32,33 |
| | *Dicotylophyllum* sp. div. | 5 | 40 | 2 | 16,33 |
| | *Ficus atlantidis* | 3 | 33.3 | 1 | 32 |
| | *Ficus truncata* | 4 | 25 | 1 | 12 |
| **Total** | | **1260** | **17.46** | **33** | **1,2,3,4,5,8,11,12,13,14,15, 16,17,32,33,34,36,41,49,50, 53,57,76,78,84,89,90,110, 117,145,201,215** |

**Table S3.** Insect and floral composition at the Clay Superseam Horizon (**CSH**); DT – damage type

| **Family rank** | **Taxon** | **Leaves** | **Damaged (%)** | **No. DT** | **DT occurrences** |
|---|---|---|---|---|---|
| Betulaceae | *Alnus gaudinii* | 2 | 50 | 2 | 14,145 |
| | *Betula* sp. | 2 | 0 | 0 | |
| Cercidiphyllaceae | *Cercidiphyllum crenatum* | 2 | 100 | 3 | 4,12,33 |
| Juglandaceae | *Juglans acuminata* | 1 | 100 | 1 | 9 |
| Lythraceae | *Decodon gibbosus* | 1 | 100 | 2 | 2,4 |
| Rhamnaceae | *Berchemia multinervis* | 1 | 0 | 0 | |
| Theaceae | *Ternstroemites* sp. | 1 | 0 | 0 | |
| Tiliaceae | *Dombeopsis lobata* | 1 | 100 | 1 | 16 |
| Sapindaceae | *Acer tricuspidatum* | 3 | 33,3 | 1 | 57 |
| Ulmaceae | *Ulmus pyramidalis* | 2 | 100 | 3 | 2,12,16 |
| **Total** | | 16 | 56.25 | 9 | 2,4,9,12,14,16,33,57,145 |

**Table S4**. Proportionality of individual taxa with number of specimens ≥ 25 at the site, together with proportionality of the damaged leaves, diversity of all DTs and FFGs and the diversity per one leaf at these taxa.

| Taxa ≥ 25 specimens | Leaves | Specimens at site % | Proportionality of damaged | SD | All types of damage | | | | FFG | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Diversity | Number of occurrences | N/leaf | SD | Diversity | Dtto/ damaged leaf |
| **LCH** | | | | | | | | | | |
| *Acer tricuspidatum* | 27 | 2.1% | 0.259 | 0.084 | 4 | 8 | 0.296 | 0.088 | 3 | 1.000 |
| *Alnus julianiformis* | 289 | 22.9% | 0.131 | 0.020 | 11 | 42 | 0.145 | 0.021 | 3 | 1.053 |
| *Comptonia difformis* | 25 | 2.0% | 0.080 | 0.054 | 1 | 2 | 0.080 | 0.054 | 1 | 1.000 |
| *Daphnogene polymorpha* | 224 | 17.8% | 0.134 | 0.023 | 7 | 34 | 0.152 | 0.024 | 4 | 1.033 |
| *Fraxinus bilinica* | 26 | 2.1% | 0.231 | 0.083 | 6 | 8 | 0.308 | 0.091 | 4 | 1.333 |
| Lauraceae gen. et sp. indet. | 175 | 13.9% | 0.171 | 0.028 | 10 | 33 | 0.189 | 0.030 | 4 | 1.100 |
| *Laurophyllum saxonicum* | 38 | 3.0% | 0.289 | 0.074 | 7 | 12 | 0.316 | 0.075 | 4 | 1.000 |
| *Laurophyllum* sp. | 84 | 6.7% | 0.214 | 0.045 | 8 | 21 | 0.250 | 0.047 | 3 | 1.111 |
| *Myrica lignitum* | 38 | 3.0% | 0.316 | 0.075 | 8 | 14 | 0.368 | 0.078 | 4 | 1.083 |
| *Myrica* sp. | 56 | 4.4% | 0.161 | 0.049 | 4 | 10 | 0.179 | 0.051 | 3 | 1.111 |
| *Nyssa haidingeri* | 46 | 3.7% | 0.043 | 0.030 | 2 | 2 | 0.043 | 0.030 | 2 | 1.000 |
| *Quercus rhenana* | 31 | 2.5% | 0.387 | 0.087 | 9 | 18 | 0.581 | 0.089 | 7 | 1.417 |
| **DSH** | | | | | | | | | | |
| *Acer angustilobum* | 35 | 1.6% | 0.286 | 0.076 | 6 | 10 | 0.286 | 0.076 | 4 | 1.000 |
| *Acer intergerrimum* | 28 | 1.3% | 0.179 | 0.072 | 6 | 8 | 0.286 | 0.085 | 5 | 1.400 |
| *Acer tricuspidatum* | 91 | 4.1% | 0.275 | 0.047 | 11 | 38 | 0.418 | 0.052 | 5 | 1.360 |
| *Alnus gaudinii* | 85 | 3.8% | 0.282 | 0.049 | 13 | 28 | 0.329 | 0.051 | 5 | 1.042 |
| *Alnus julianiformis* | 166 | 7.4% | 0.319 | 0.036 | 19 | 69 | 0.416 | 0.038 | 5 | 1.170 |
| *Berberis berberidifolia* | 55 | 2.5% | 0.145 | 0.048 | 7 | 10 | 0.182 | 0.052 | 4 | 1.125 |
| *Betula* sp. | 32 | 1.4% | 0.406 | 0.087 | 7 | 16 | 0.500 | 0.088 | 4 | 1.154 |
| *Carya* sp. | 60 | 2.7% | 0.433 | 0.064 | 10 | 39 | 0.650 | 0.062 | 4 | 1.310 |
| *Cercidiphyllum crenatum* | 32 | 1.4% | 0.156 | 0.064 | 5 | 7 | 0.219 | 0.073 | 3 | 1.400 |
| cf. *Alnus* sp. | 31 | 1.4% | 0.194 | 0.071 | 6 | 7 | 0.226 | 0.075 | 2 | 1.000 |
| *Comptonia difformis* | 45 | 2.0% | 0.133 | 0.051 | 1 | 6 | 0.133 | 0.051 | 1 | 1.000 |
| *Daphnogene polymorpha* | 83 | 3.7% | 0.229 | 0.046 | 11 | 22 | 0.265 | 0.048 | 4 | 1.105 |
| *Decodon gibbosus* | 33 | 1.5% | 0.394 | 0.085 | 9 | 17 | 0.515 | 0.087 | 5 | 1.231 |
| *Ficus truncata* | 53 | 2.4% | 0.226 | 0.057 | 5 | 14 | 0.264 | 0.061 | 3 | 1.167 |
| *Fraxinus bilinica* | 49 | 2.2% | 0.306 | 0.066 | 10 | 20 | 0.408 | 0.070 | 4 | 1.267 |
| Lauraceae gen. et sp. indet. | 78 | 3.5% | 0.141 | 0.039 | 8 | 13 | 0.167 | 0.042 | 2 | 1.091 |
| Leguminosae gen. et sp .indet. | 51 | 2.3% | 0.196 | 0.056 | 6 | 10 | 0.196 | 0.056 | 3 | 1.000 |
| *Liquidambar europaea* | 53 | 2.4% | 0.264 | 0.061 | 7 | 17 | 0.321 | 0.064 | 4 | 1.214 |
| *Nyssa haidingeri* | 87 | 3.9% | 0.207 | 0.043 | 15 | 27 | 0.310 | 0.050 | 4 | 1.333 |
| *Pailiurus tiliaefolius* | 36 | 1.6% | 0.194 | 0.066 | 4 | 8 | 0.222 | 0.069 | 2 | 1.143 |
| *Parrotia pristina* | 66 | 3.0% | 0.303 | 0.057 | 9 | 28 | 0.424 | 0.061 | 5 | 1.400 |
| *Podocarpium podocarpum* | 64 | 2.9% | 0.125 | 0.041 | 8 | 11 | 0.172 | 0.047 | 5 | 1.375 |
| *Populus populina* | 29 | 1.3% | 0.310 | 0.086 | 5 | 11 | 0.379 | 0.090 | 2 | 1.222 |
| *Populus zaddachii* | 37 | 1.7% | 0.568 | 0.081 | 15 | 30 | 0.811 | 0.064 | 6 | 1.286 |
| *Quercus rhenana* | 33 | 1.5% | 0.242 | 0.075 | 8 | 14 | 0.424 | 0.086 | 4 | 1.500 |
| *Rosa europaea* | 27 | 1.2% | 0.074 | 0.050 | 2 | 2 | 0.074 | 0.050 | 1 | 1.000 |
| *Rubus merianii* | 25 | 1.1% | 0.160 | 0.073 | 5 | 5 | 0.200 | 0.080 | 2 | 1.250 |
| *Salix haidingeri* | 46 | 2.1% | 0.326 | 0.069 | 11 | 19 | 0.413 | 0.073 | 6 | 1.133 |
| *Sapindus falcifolius* | 27 | 1.2% | 0.148 | 0.068 | 4 | 5 | 0.185 | 0.075 | 3 | 1.250 |
| *Ternstroemites* sp. | 59 | 2.6% | 0.271 | 0.058 | 9 | 26 | 0.441 | 0.065 | 5 | 1.563 |
| *Ulmus pyramidalis* | 118 | 5.3% | 0.144 | 0.032 | 8 | 19 | 0.161 | 0.034 | 4 | 1.059 |
| *Zelkova zelkovifolia* | 56 | 2.5% | 0.179 | 0.051 | 7 | 14 | 0.250 | 0.058 | 3 | 1.100 |

**Table S5.** Specialized damage, Galling and Mining – their total diversity, number of occurrences and number of occurrences per one leaf at the taxa with 25 and more specimens.

| Taxa ≥ 25 specimens | Specialized types of damage | | | | Galling | | | | Mining | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Diversity | Number of occurrences | N/leaf | SD | Diversity | Number of occurrences | N/leaf | SD | Diversity | Number of occurrences | N/leaf | SD |
| **LCH** | | | | | | | | | | | | |
| *Acer tricuspidatum* | 2 | 6 | 0.222 | 0.080 | 2 | 6 | 0.222 | 0.080 | 0 | 0 | 0 | 0 |
| *Alnus julianiformis* | 5 | 19 | 0.066 | 0.015 | 4 | 18 | 0.062 | 0.014 | 0 | 0 | 0 | 0 |
| *Comptonia difformis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Daphnogene polymorpha* | 4 | 26 | 0.116 | 0.021 | 3 | 25 | 0.112 | 0.021 | 1 | 1 | 0.004 | 0.004 |
| *Fraxinus bilinica* | 4 | 6 | 0.231 | 0.083 | 3 | 5 | 0.192 | 0.077 | 1 | 1 | 0.038 | 0.038 |
| Lauraceae gen. et sp. indet. | 4 | 12 | 0.069 | 0.019 | 3 | 9 | 0.051 | 0.017 | 0 | 0 | 0 | 0 |
| *Laurophyllum saxonicum* | 3 | 4 | 0.105 | 0.050 | 3 | 4 | 0.105 | 0.050 | 0 | 0 | 0 | 0 |
| *Laurophyllum* sp. | 3 | 5 | 0.060 | 0.026 | 4 | 6 | 0.071 | 0.028 | 0 | 0 | 0 | 0 |
| *Myrica lignitum* | 3 | 3 | 0.079 | 0.044 | 1 | 1 | 0.026 | 0.026 | 2 | 2 | 0.053 | 0.036 |
| *Myrica* sp. | 1 | 1 | 0.018 | 0.018 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Nyssa haidingeri* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Quercus rhenana* | 4 | 7 | 0.226 | 0.075 | 3 | 6 | 0.194 | 0.071 | 1 | 1 | 0.032 | 0.032 |
| **DSH** | | | | | | | | | | | | |
| *Acer angustilobum* | 1 | 1 | 0.029 | 0.028 | 1 | 1 | 0.029 | 0.028 | 0 | 0 | 0 | 0 |
| *Acer intergerrimum* | 2 | 2 | 0.071 | 0.049 | 1 | 1 | 0.036 | 0.035 | 1 | 1 | 0.036 | 0.035 |
| *Acer tricuspidatum* | 4 | 4 | 0.044 | 0.021 | 0 | 0 | 0 | 0 | 2 | 2 | 0.022 | 0.015 |
| *Alnus gaudinii* | 6 | 6 | 0.071 | 0.028 | 4 | 4 | 0.047 | 0.023 | 1 | 1 | 0.012 | 0.012 |
| *Alnus julianiformis* | 7 | 10 | 0.060 | 0.018 | 3 | 6 | 0.036 | 0.014 | 2 | 2 | 0.012 | 0.008 |
| *Berberis berberidifolia* | 1 | 1 | 0.018 | 0.018 | 0 | 0 | 0 | 0 | 1 | 1 | 0.018 | 0.018 |
| *Betula* sp. | 0 | 0 | 0 | 0 | 1 | 1 | 0.031 | 0.031 | 0 | 0 | 0 | 0 |
| *Carya* sp. | 3 | 4 | 0.067 | 0.032 | 5 | 6 | 0.100 | 0.039 | 0 | 0 | 0 | 0 |
| *Cercidiphyllum crenatum* | 1 | 1 | 0.031 | 0.031 | 2 | 3 | 0.094 | 0.052 | 0 | 0 | 0 | 0 |
| cf. *Alnus* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Comptonia difformis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Daphnogene polymorpha* | 4 | 5 | 0.060 | 0.026 | 2 | 3 | 0.036 | 0.020 | 0 | 0 | 0 | 0 |
| *Decodon gibbosus* | 3 | 4 | 0.121 | 0.057 | 3 | 4 | 0.121 | 0.057 | 0 | 0 | 0 | 0 |
| *Ficus truncata* | 1 | 1 | 0.019 | 0.019 | 1 | 1 | 0.019 | 0.019 | 0 | 0 | 0 | 0 |
| *Fraxinus bilinica* | 4 | 5 | 0.102 | 0.043 | 5 | 7 | 0.143 | 0.050 | 0 | 0 | 0 | 0 |
| Lauraceae gen. et sp. indet. | 2 | 2 | 0.026 | 0.018 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Leguminosae gen. et sp .indet. | 1 | 1 | 0.020 | 0.019 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Liquidambar europaea* | 2 | 4 | 0.075 | 0.036 | 0 | 0 | 0 | 0 | 2 | 4 | 0.075 | 0.036 |
| *Nyssa haidingeri* | 5 | 5 | 0.057 | 0.025 | 2 | 2 | 0.023 | 0.016 | 0 | 0 | 0 | 0 |
| *Pailiurus tiliaefolius* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Parrotia pristina* | 1 | 1 | 0.015 | 0.015 | 1 | 1 | 0.015 | 0.015 | 0 | 0 | 0 | 0 |
| *Podocarpium podocarpum* | 1 | 2 | 0.031 | 0.022 | 1 | 2 | 0.031 | 0.022 | 0 | 0 | 0 | 0 |
| *Populus populina* | 1 | 2 | 0.069 | 0.047 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Populus zaddachii* | 7 | 9 | 0.243 | 0.071 | 3 | 3 | 0.081 | 0.045 | 1 | 1 | 0.027 | 0.027 |
| *Quercus rhenana* | 3 | 3 | 0.091 | 0.050 | 1 | 1 | 0.030 | 0.030 | 2 | 2 | 0.061 | 0.042 |
| *Rosa europaea* | 1 | 1 | 0.037 | 0.036 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Rubus merianii* | 1 | 1 | 0.040 | 0.039 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Salix haidingeri* | 3 | 3 | 0.065 | 0.036 | 2 | 2 | 0.043 | 0.030 | 0 | 0 | 0 | 0 |
| *Sapindus falcifolius* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ternstroemites* sp. | 2 | 3 | 0.051 | 0.029 | 1 | 1 | 0.017 | 0.017 | 0 | 0 | 0 | 0 |
| *Ulmus pyramidalis* | 1 | 1 | 0.008 | 0.008 | 0 | 0 | 0 | 0 | 1 | 1 | 0.008 | 0.008 |
| *Zelkova zelkovifolia* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**Table S6.** Mean diversities of selected categories of damage rarified to 25 leaves of each taxa.

| Taxa ≥ 25 specimens | All types of damage | | Functional feeding groups | | Specialized types of damages | | Galling | | Mining | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Diversity | SD | Diversity | SD | Diversity | SD | Diversity | SD | Diversity | SD |
| **LCH** | | | | | | | | | | |
| *Acer tricuspidatum* | 2.848 | 0.855 | 2.194 | 0.697 | 1.616 | 0.499 | 1.600 | 0.502 | 0 | 0 |
| *Alnus julianiformis* | 2.738 | 1.178 | 1.890 | 0.734 | 1.234 | 0.751 | 1.146 | 0.771 | 0 | 0 |
| *Comptonia difformis* | 0.898 | 0.303 | 0.900 | 0.300 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Daphnogene polymorpha* | 2.450 | 1.065 | 1.810 | 0.804 | 1.648 | 0.781 | 1.542 | 0.714 | 0.096 | 0.295 |
| *Fraxinus bilinica* | 3.946 | 1.563 | 2.864 | 1.455 | 2.812 | 0.831 | 2.194 | 0.705 | 0.606 | 0.489 |
| Lauraceae gen. et sp. indet. | 3.218 | 1.301 | 2.310 | 0.822 | 1.358 | 0.874 | 0.992 | 0.762 | 0 | 0 |
| *Laurophyllum saxonicum* | 4.370 | 1.246 | 3.138 | 0.696 | 1.672 | 0.816 | 1.758 | 0.823 | 0 | 0 |
| *Laurophyllum* sp. | 3.786 | 1.336 | 2.556 | 0.610 | 1.076 | 0.779 | 1.410 | 0.907 | 0 | 0 |
| *Myrica lignitum* | 4.820 | 1.463 | 3.136 | 0.712 | 1.516 | 0.824 | 0.506 | 0.500 | 0.966 | 0.731 |
| *Myrica* sp. | 2.570 | 0.898 | 2.280 | 0.715 | 0.362 | 0.481 | 0 | 0 | 0 | 0 |
| *Nyssa haidingeri* | 0.798 | 0.671 | 0.794 | 0.710 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Quercus rhenana* | 6.678 | 1.465 | 5.356 | 1.010 | 2.790 | 0.949 | 2.268 | 0.760 | 0.534 | 0.499 |
| **DSH** | | | | | | | | | | |
| *Acer angustilobum* | 3.626 | 1.099 | 2.550 | 0.840 | 0.504 | 0.500 | 0.514 | 0.500 | 0 | 0 |
| *Acer intergerrimum* | 3.810 | 1.709 | 3.310 | 1.245 | 1.230 | 0.680 | 0.582 | 0.494 | 0.608 | 0.489 |
| *Acer tricuspidatum* | 5.036 | 1.660 | 2.928 | 0.953 | 1.014 | 0.834 | 0 | 0 | 0.448 | 0.566 |
| *Alnus gaudinii* | 5.076 | 1.508 | 3.158 | 0.855 | 1.524 | 1.029 | 0.976 | 0.849 | 0.240 | 0.428 |
| *Alnus julianiformis* | 6.576 | 1.686 | 3.316 | 0.798 | 1.388 | 1.045 | 0.742 | 0.724 | 0.304 | 0.498 |
| *Berberis berberidifolia* | 3.168 | 1.372 | 2.396 | 0.932 | 0.310 | 0.463 | 0 | 0 | 0.404 | 0.491 |
| *Betula* sp. | 5.052 | 1.173 | 3.022 | 0.715 | 0 | 0 | 0.564 | 0.496 | 0 | 0 |
| *Carya* sp. | 5.864 | 1.249 | 3.276 | 0.552 | 1.246 | 0.841 | 1.926 | 1.054 | 0 | 0 |
| *Cercidiphyllum crenatum* | 3.258 | 1.199 | 2.526 | 0.680 | 0.518 | 0.500 | 1.338 | 0.639 | 0 | 0 |
| cf. *Alnus* sp. | 3.632 | 1.201 | 1.554 | 0.510 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Comptonia difformis* | 0.978 | 0.147 | 0.956 | 0.205 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Daphnogene polymorpha* | 4.472 | 1.430 | 2.684 | 0.788 | 1.222 | 0.884 | 0.728 | 0.650 | 0 | 0 |
| *Decodon gibbosus* | 5.956 | 1.187 | 3.990 | 0.723 | 1.868 | 0.767 | 1.890 | 0.802 | 0 | 0 |
| *Ficus truncata* | 2.914 | 0.998 | 2.140 | 0.778 | 0.410 | 0.492 | 0.392 | 0.489 | 0 | 0 |
| *Fraxinus bilinica* | 5.652 | 1.388 | 3.274 | 0.623 | 1.864 | 0.931 | 2.590 | 1.101 | 0 | 0 |
| Lauraceae gen. et sp. indet. | 3.004 | 1.439 | 1.720 | 0.504 | 0.578 | 0.676 | 0 | 0 | 0 | 0 |
| Leguminosae gen. et sp .indet. | 3.200 | 1.118 | 1.974 | 0.703 | 0.388 | 0.488 | 0 | 0 | 0 | 0 |
| *Liquidambar europaea* | 4.066 | 1.326 | 3.394 | 0.710 | 1.234 | 0.666 | 0 | 0 | 1.186 | 0.710 |
| *Nyssa haidingeri* | 5.688 | 2.004 | 2.738 | 0.860 | 1.242 | 0.921 | 0.498 | 0.602 | 0 | 0 |
| *Pailiurus tiliaefolius* | 2.938 | 0.846 | 1.734 | 0.456 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Parrotia pristina* | 5.182 | 1.307 | 3.334 | 0.817 | 0.308 | 0.462 | 0.306 | 0.461 | 0 | 0 |
| *Podocarpium podocarpum* | 3.360 | 1.633 | 2.836 | 1.073 | 0.518 | 0.500 | 0.540 | 0.499 | 0 | 0 |
| *Populus populina* | 4.036 | 0.994 | 1.932 | 0.252 | 0.840 | 0.367 | 0 | 0 | 0 | 0 |
| *Populus zaddachii* | 9.664 | 1.735 | 4.712 | 0.824 | 3.892 | 1.333 | 1.502 | 0.831 | 0.486 | 0.500 |
| *Quercus rhenana* | 5.380 | 1.411 | 3.282 | 0.737 | 1.560 | 0.820 | 0.558 | 0.497 | 1.040 | 0.660 |
| *Rosa europaea* | 1.238 | 0.656 | 0.854 | 0.353 | 0.590 | 0.492 | 0 | 0 | 0 | 0 |
| *Rubus merianii* | 3.226 | 1.232 | 1.816 | 0.422 | 0.598 | 0.491 | 0 | 0 | 0 | 0 |
| *Salix haidingeri* | 5.870 | 1.598 | 4.082 | 1.042 | 1.254 | 0.846 | 0.772 | 0.682 | 0 | 0 |
| *Sapindus falcifolius* | 2.688 | 0.974 | 2.298 | 0.728 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ternstroemites* sp. | 5.320 | 1.320 | 3.614 | 0.763 | 0.964 | 0.675 | 0.336 | 0.473 | 0 | 0 |
| *Ulmus pyramidalis* | 2.920 | 1.344 | 2.008 | 0.773 | 0.162 | 0.369 | 0 | 0 | 0.188 | 0.391 |
| *Zelkova zelkovifolia* | 3.518 | 1.355 | 2.184 | 0.638 | 0 | 0 | 0 | 0 | 0 | 0 |

**Table S7.** Mean diversities of selected categories of damage rarified to their 5 own occurrences at each taxa.

| Taxa ≥ 25 specimens | All types of damage | | Functional feeding groups | | Specialized types of damages | | Galling | | Mining | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Diversity | SD | Diversity | SD | Diversity | SD | Diversity | SD | Diversity | SD |
| **LCH** | | | | | | | | | | |
| *Acer tricuspidatum* | 2.473 | 0.759 | 1.944 | 0.677 | 1.602 | 0.490 | 1.596 | 0.491 | 0 | 0 |
| *Alnus julianiformis* | 3.566 | 0.854 | 2.293 | 0.526 | 2.464 | 0.749 | 2.277 | 0.642 | 0 | 0 |
| *Comptonia difformis* | 1.000 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Daphnogene polymorpha* | 3.012 | 0.763 | 2.047 | 0.701 | 2.262 | 0.584 | 2.085 | 0.444 | 1.000 | 0 |
| *Fraxinus bilinica* | 3.342 | 0.821 | 2.483 | 0.762 | 2.750 | 0.720 | 2.336 | 0.618 | 1.000 | 0 |
| Lauraceae gen. et sp. indet. | 3.362 | 0.888 | 2.492 | 0.650 | 2.866 | 0.650 | 2.308 | 0.534 | 0 | 0 |
| *Laurophyllum saxonicum* | 3.483 | 0.819 | 2.859 | 0.651 | 2.500 | 0.565 | 2.498 | 0.558 | 0 | 0 |
| *Laurophyllum* sp. | 3.420 | 0.849 | 2.507 | 0.554 | 2.381 | 0.610 | 2.751 | 0.712 | 0 | 0 |
| *Myrica lignitum* | 3.515 | 0.845 | 2.629 | 0.695 | 2.593 | 0.522 | 1.000 | 0 | 1.953 | 0.212 |
| *Myrica* sp. | 2.863 | 0.661 | 2.500 | 0.551 | 1.000 | 0 | 0 | 0 | 0 | 0 |
| *Nyssa haidingeri* | 1.942 | 0.235 | 1.942 | 0.234 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Quercus rhenana* | 3.769 | 0.775 | 3.363 | 0.819 | 2.829 | 0.684 | 2.433 | 0.571 | 1.000 | 0 |
| **DSH** | | | | | | | | | | |
| *Acer angustilobum* | 2.999 | 0.863 | 2.236 | 0.769 | 1.000 | 0 | 1.000 | 0 | 0 | 0 |
| *Acer intergerrimum* | 3.348 | 0.808 | 2.865 | 0.814 | 1.930 | 0.255 | 1.000 | 0 | 1.000 | 0 |
| *Acer tricuspidatum* | 3.393 | 0.869 | 2.330 | 0.712 | 3.063 | 0.637 | 0 | 0 | 1.931 | 0.254 |
| *Alnus gaudinii* | 3.737 | 0.859 | 2.626 | 0.797 | 3.603 | 0.735 | 3.043 | 0.654 | 1.000 | 0 |
| *Alnus julianiformis* | 3.989 | 0.796 | 2.589 | 0.686 | 3.536 | 0.787 | 2.439 | 0.559 | 1.928 | 0.259 |
| *Berberis berberidifolia* | 3.558 | 0.794 | 2.704 | 0.722 | 1.000 | 0 | 0 | 0 | 1.000 | 0 |
| *Betula* sp. | 3.373 | 0.821 | 2.397 | 0.671 | 0 | 0 | 1.000 | 0 | 0 | 0 |
| *Carya* sp. | 3.304 | 0.853 | 2.513 | 0.617 | 2.490 | 0.570 | 3.270 | 0.741 | 0 | 0 |
| *Cercidiphyllum crenatum* | 3.222 | 0.734 | 2.566 | 0.528 | 1.000 | 0 | 1.869 | 0.337 | 0 | 0 |
| cf. *Alnus* sp. | 3.508 | 0.777 | 1.540 | 0.499 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Comptonia difformis* | 1.000 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Daphnogene polymorpha* | 3.778 | 0.824 | 2.495 | 0.669 | 2.924 | 0.688 | 1.848 | 0.359 | 0 | 0 |
| *Decodon gibbosus* | 3.605 | 0.845 | 2.976 | 0.717 | 2.504 | 0.559 | 2.499 | 0.558 | 0 | 0 |
| *Ficus truncata* | 2.620 | 0.783 | 2.010 | 0.623 | 1.000 | 0 | 1.000 | 0 | 0 | 0 |
| *Fraxinus bilinica* | 3.701 | 0.830 | 2.736 | 0.635 | 2.934 | 0.696 | 3.263 | 0.732 | 0 | 0 |
| Lauraceae gen. et sp. indet. | 3.672 | 0.796 | 1.939 | 0.239 | 1.934 | 0.248 | 0 | 0 | 0 | 0 |
| Leguminosae gen. et sp .indet. | 3.425 | 0.783 | 2.092 | 0.635 | 1.000 | 0 | 0 | 0 | 0 | 0 |
| *Liquidambar europaea* | 3.321 | 0.817 | 2.903 | 0.659 | 1.942 | 0.235 | 0 | 0 | 1.934 | 0.248 |
| *Nyssa haidingeri* | 4.213 | 0.731 | 2.513 | 0.740 | 3.333 | 0.699 | 1.938 | 0.242 | 0 | 0 |
| *Pailiurus tiliaefolius* | 2.932 | 0.672 | 1.787 | 0.410 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Parrotia pristina* | 3.501 | 0.782 | 2.572 | 0.765 | 1.000 | 0 | 1.000 | 0 | 0 | 0 |
| *Podocarpium podocarpum* | 3.804 | 0.786 | 3.188 | 0.757 | 1.000 | 0 | 1.000 | 0 | 0 | 0 |
| *Populus populina* | 3.166 | 0.739 | 1.804 | 0.397 | 1.000 | 0 | 0 | 0 | 0 | 0 |
| *Populus zaddachii* | 4.007 | 0.792 | 2.617 | 0.840 | 3.523 | 0.818 | 2.613 | 0.510 | 1.000 | 0 |
| *Quercus rhenana* | 3.616 | 0.796 | 2.692 | 0.658 | 2.626 | 0.502 | 1.000 | 0 | 1.942 | 0.235 |
| *Rosa europaea* | 1.940 | 0.238 | 1.000 | 0 | 1.000 | 0 | 0 | 0 | 0 | 0 |
| *Rubus merianii* | 3.368 | 0.718 | 1.919 | 0.274 | 1.000 | 0 | 0 | 0 | 0 | 0 |
| *Salix haidingeri* | 3.718 | 0.846 | 3.038 | 0.802 | 2.607 | 0.508 | 1.938 | 0.242 | 0 | 0 |
| *Sapindus falcifolius* | 2.948 | 0.669 | 2.518 | 0.538 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Ternstroemites* sp. | 3.510 | 0.796 | 2.755 | 0.710 | 1.866 | 0.341 | 1.000 | 0 | 0 | 0 |
| *Ulmus pyramidalis* | 3.545 | 0.806 | 2.311 | 0.637 | 1.000 | 0 | 0 | 0 | 1.000 | 0 |
| *Zelkova zelkovifolia* | 3.267 | 0.809 | 2.207 | 0.512 | 0 | 0 | 0 | 0 | 0 | 0 |

**Table S8.** Total number of leaves together of number of leaves affected by distinct FFGs and the mean $M_A$ of the each taxa.

| Taxa ≥ 25 specimens | Leaves | Number of the damaged leaves | | | | | | | | $M_A$ [$gm^{-2}$] |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Hole feeding | Marginal feeding | Skeleton. | Surface feeding | Galling | Mining | Pierc. & Sucking. | Oviposition | |
| **LCH** | | | | | | | | | | |
| *Acer tricuspidatum* | 27 | 18 | 4 | 0 | 0 | 18 | 0 | 0 | 0 | 69 |
| *Alnus julianiformis* | 289 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 136 |
| *Comptonia difformis* | 25 | 3 | 5 | 0 | 0 | 22 | 1 | 0 | 0 | 107 |
| *Daphnogene polymorpha* | 224 | 1 | 1 | 0 | 0 | 5 | 1 | 0 | 0 | 53 |
| *Fraxinus bilinica* | 26 | 5 | 18 | 0 | 1 | 9 | 0 | 0 | 0 | 99 |
| Lauraceae gen. et sp. indet. | 175 | 2 | 4 | 0 | 1 | 4 | 0 | 0 | 0 | 92 |
| *Laurophyllum saxonicum* | 38 | 4 | 10 | 0 | 0 | 6 | 0 | 0 | 0 | 137 |
| *Laurophyllum* sp | 84 | 3 | 7 | 0 | 0 | 1 | 2 | 0 | 0 | 146 |
| *Myrica lignitum* | 38 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 109 |
| *Nyssa haidingeri* | 46 | 4 | 3 | 1 | 2 | 5 | 1 | 0 | 1 | 104 |
| *Quercus rhenana* | 31 | 0 | 1 | 0 | 1 | 5 | 0 | 0 | 0 | 71 |
| **DSH** | | | | | | | | | | |
| *Acer angustilobum* | 35 | 3 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 86 |
| *Acer intergerrimum* | 28 | 21 | 8 | 1 | 2 | 0 | 2 | 0 | 0 | 82 |
| *Acer tricuspidatum* | 91 | 13 | 5 | 0 | 2 | 4 | 1 | 0 | 0 | 51 |
| *Alnus gaudinii* | 85 | 29 | 21 | 0 | 4 | 6 | 2 | 0 | 0 | 63 |
| *Alnus julianiformis* | 166 | 2 | 4 | 0 | 2 | 0 | 1 | 0 | 0 | 146 |
| *Berberis berberidifolia* | 55 | 9 | 4 | 0 | 1 | 1 | 0 | 0 | 0 | 80 |
| *Betula* sp. | 32 | 16 | 11 | 0 | 1 | 6 | 0 | 0 | 0 | 77 |
| *Carya* sp. | 60 | 2 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 134 |
| *Cercidiphyllum crenatum* | 32 | 5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 80 |
| cf. *.Alnus* sp. | 31 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 77 |
| *Comptonia difformis* | 45 | 11 | 6 | 0 | 1 | 3 | 0 | 0 | 0 | 86 |
| *Daphnogene polymorpha* | 83 | 5 | 5 | 1 | 1 | 4 | 0 | 0 | 0 | 114 |
| *Decodon gibbosus* | 33 | 6 | 5 | 0 | 1 | 7 | 0 | 0 | 0 | 53 |
| *Fraxinus bilinica* | 49 | 6 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 102 |
| Lauraceae gen. et sp. indet. | 78 | 7 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 59 |
| Leguminosae gen. et sp. indet. | 51 | 5 | 2 | 0 | 6 | 0 | 4 | 0 | 0 | 59 |
| *Liquidambar europaea* | 53 | 14 | 3 | 0 | 5 | 2 | 0 | 0 | 0 | 67 |
| *Nyssa haidingeri* | 87 | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 73 |
| *Pailiurus tiliaefolius* | 36 | 16 | 6 | 1 | 4 | 1 | 0 | 0 | 0 | 68 |
| *Parrotia pristina* | 66 | 8 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 68 |
| *Populus populina* | 29 | 15 | 4 | 1 | 3 | 3 | 1 | 0 | 0 | 68 |
| *Populus zaddachii* | 37 | 5 | 4 | 0 | 0 | 1 | 2 | 0 | 0 | 91 |
| *Quercus rhenana* | 33 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 64 |
| *Rosa europaea* | 27 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 72 |
| *Rubus merianii* | 25 | 4 | 7 | 1 | 2 | 2 | 0 | 0 | 1 | 102 |
| *Salix haidingeri* | 46 | 2 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 63 |
| *Sapindus falcifolius* | 27 | 5 | 11 | 1 | 7 | 1 | 0 | 0 | 0 | 101 |
| *Ternstroemites* sp. | 59 | 11 | 5 | 0 | 1 | 0 | 1 | 0 | 0 | 72 |
| *Ulmus pyramidalis* | 118 | 7 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 67 |

## Článek II

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Research paper

# Galls and gall makers on plant leaves from the lower Miocene (Burdigalian) of the Czech Republic: Systematic and palaeoecological implications

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ABSTRACT

A detailed study of more than 4000 plant macrofossils from the lower Miocene of the Most Basin (localities Bílina Mine and Břešťany) in northern Bohemia has been made in order to implement quantitative and taxonomic analyses of gall occurrences. Fourteen distinct arthropods were identified as possible causers of fossil galls. Similarities in the form, size and position on the host-plant leaves allowed identifications at least to the generic level and to discuss their relationships to extant gall-inducing species that cause morphologically similar galls on related host-plant species. The fossil galls were induced by members belonging to the following insect and mite families: Psyllidae (Hemiptera), Cecidomyiidae (Diptera), Cynipidae (Hymenoptera) and Eriophyidae (Acari). Galls on *Taxodium* induced by gall midges of the genus *Taxodiomyia* (Diptera: Cecidomyiidae) are recorded for the first time. All here described galls are the first records of fossil galls from the Neogene of the Central Europe and complement the view plant–insect interactions during the lower Miocene. The Bílina Mine collection comprises material from several fossiliferous layers representing also different ecosystem types. The presence of elevated gall frequency in the Lake Clayey Horizon (LCH) accompanied by the lower diversity of the other damage types implies colder and drier habitat with unevenly distributed rainfall in comparison with Delta Sandy Horizon (DSH).



## 1. Introduction

Galls are remarkable structures, which may occur on roots, stems, leaves, flower buds and flowers and on fruits of various plants. Most are cause by parasitic insects, but the formation of galls can also be induced by viruses, bacteria, fungi, nematodes, and mites (Price et al., 1987; Stone and Schönrogge, 2003). The ability of organisms to induce galls on plants has evolved independently many times during the evolution of insects as well as of other groups, with over 13,000 described species with this habit (e.g., Shorthouse and Rohfritsch, 1992; Williams, 1994; Crespi et al., 1997; Raman et al., 2005a). Galls are believed to provide the inducer with enhanced nutrition, a favorable microclimate and, in some cases, protection from natural enemies (Stone and Schönrogge, 2003). Insect galls are thus an extended phenotype of their inducers — with the gall exposed to selection pressures related to predation and host resistance (Dawkins, 1982; Stone and Schönrogge, 2003). About 80% of the insect galls are found on leaves, but the first documented occurrence in the fossil record is on plant stems (Labandeira, 1998).

Nearly three thousand extant gall-causing and associated organisms are known from Central and Northern Europe (Buhr, 1964–1965). They belong to various groups of organisms: about one third to bacteria and fungi, two-thirds to animals. Three groups of animals are the species richest causers of galls on various plants: (i) the gall midges (Cecidomyiidae, Diptera) with about 600 species; (ii) eriophyid mites (Eriophyoidea, Acarina) with about 350 species and (iii) aphids (Aphidoidea, Hemiptera) with about 370 species. Since that time many new species of gall-causing organisms have been discovered and described and the number of these organisms is at present much higher. Due to prevailing subtropical climatic conditions in Neogene of Central Europe it can be supposed that there was higher insect diversity including probably some other gall inducing taxa like thrips (Thysanoptera).

In this paper we describe the induced fossil plant galls from the lower Miocene of the Most Basin in the northern Bohemia and implement a quantitative and taxonomic analysis of gall occurrences. These galls are two- or three-dimensional impressions, preserved as remains or traces found on various plant organs, most frequently on leaves. On the basis of the gall similarities in the form, size and their position on the leaves of the fossil host plants it was possible to identify their taxonomical group to at least generic level and to ascribe their relationships to gall-inducing species that currently cause morphologically similar galls on related host plant species. It is likely that some causers of Neogene galls are tightly related to their recent relatives, since the

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insect fauna of that time, shows close similarity with the recent one (Grimaldi and Engel, 2005).

## 2. Overview on the history of fossil leaves with galls

The study of galls has a long history. The famous Italian physician and researcher Marcello Malpighi, the founder of microscopic anatomy, is considered to be also the founder of cecidology. Malpighi (1675) published the comprehensive work "Anatome Plantarum", in which he included the chapter called "De Gallis" (in English: About galls). The literature on galls is very extensive. For summaries of our knowledge on galls we refer to: Houard (1908–1909, 1922–1923), Felt (1940), Mani (1964, 2000), Buhr (1964–1965), Ananthakrishnan (1984), Shorthouse and Rohfritsch (1992), Yukawa and Masuda (1996), Redfern et al. (2002), Raman et al. (2005a,b), Ozaki et al. (2006).

There is not too much data on fossil galls induced by various organisms on organs host plants. Nevertheless, galling associations have a long evolutionary history reaching back to the late Palaeozoic. Gall-inducing insects were already present during the Pennsylvanian, ~300 million years ago (Labandeira and Phillips, 1996), but galling types became more common and diverse with the initial adaptive angiosperm radiation at the beginning of Late Cretaceous (Scott et al., 1994; Labandeira, 2006; Krassilov, 2008). Larew (1992) included 63 findings in his summary of fossil galls. One of the richest collections of fossil galls, including 34 impressions, was described by Straus (1977) from the upper Pliocene of Willershausen in the Harz Mountains, Germany. He ascribed them to seven groups of organisms: Fungi (2 impressions), Eriophyidae (12), Eriosomatidae (1), Aphidae (1), Adelgidae (1), Cecidomyiidae (6) and Cynipidae (3). More specimens were reported by Titchener (1999), who studied on all types of plant–insect interactions from this locality. Scott et al. (1994) examined more than 14,000 leaves of angiosperms from Cretaceous, Paleogene and Neogene localities. They described 25 types of galls on leaves of various angiosperms together with rough identifications of the gall-causers and in some cases establishing their recent relatives, particularly of families such as Cecidomyiidae, Cynipidae, Psyllidae and Eriophyidae.

Apart from angiosperms, insect-induced galls have also been described from organs of various gymnosperms. For instance, Möhn (1960) discovered the fossil gall midge species *Sequoiomyia kraeuseli* Möhn, 1960 in the seeds of *Sequoia langsdorfii* (Brongniart) Heer, 1868 (Taxodiaceae) from the Miocene of the Rhineland (Germany) and described larvae and pupae of this gall midge. This is one of the rare cases, where the causer of fossil gall is known. Galls are rather common on broad-leaved angiosperms plants, since this group is much more diverse than gymnosperms.

In the Miocene of Spain Villalta (1957) found fossil galls on leaves of *Quercus drymeja* Unger, 1845 and ascribed them to two species of eriophyid mites. He described fossil galls on leaf of *Fagus castaneaefolia* Unger, 1845 as the species *Mikiola pontiensis* Villalta, 1957. However, these galls were probably caused by another recent gall midge species — *Phegomyia fagicola* Kieffer, 1913 (Skuhravá, 2006). Straus (1977) assumed that impressions on *Betula* L., 1753 leaves were caused by *Contarinia carpini* Kieffer, 1897. The galls on *Betula* leaves were caused by another species because *Contarinia carpini* is specifically associated with *Carpinus* L., 1753.

Diéguez et al. (1996) identified thirteen types of fossil galls on leaves of eleven host plants, belonging to five plant families from the upper Miocene of La Cerdaña in northern Spain. Six of these fossil galls were considered to have been induced by Eriophyidae (Acari), three by Cecidomyiidae (Diptera) and two by Cynipidae (Hymenoptera). Waggoner and Poteet (1996) described unusual elongated galls on the leaf of *Quercus hannibali* Dorf, 1936 from the Miocene of North America, which were attributed to perpetrators of the family Cynipidae (Hymenoptera). In last few years, impressive records have been reported from the Neogene of North America. There are two leaves of *Quercus simulata* Knowlton, 1898 known from the middle Miocene of Oregon (USA), each with another type of gall, belonging to *Antronoides cyanomontana* Erwin et Schick 2007 and *A. oregonensis* Erwin et Schick, 2007 (Erwin and Schick, 2007).

Studies of fossil insect galls are tightly interconnected with other research of plant–insect associations, which advanced very rapidly in recent years. Current approaches involve many aspects and are based on different case studies, which greatly contribute to our knowledge of ancient environments (Wappler, 2010; Wappler et al., 2012). The palaeoecological, palaeoclimatological and the palaeogeographical implications are of the great importance (Wilf and Labandeira, 1999; Wilf et al., 2005, 2006; Wappler et al., 2009; Currano et al., 2010; Paik et al., 2012). Some of these studies emphasise the long-term evolutionary coexistence of the plant host and arthropod gallers (Erwin and Schick, 2007; Wappler et al., 2010) and miners (Opler, 1982; Winkler et al., 2010).

## 3. Material and methods

The material studied belongs to the collections of the Bílina Mine enterprise and the National Museum in Prague, comprising almost 4300 specimens of various plant fossils of early Miocene age, collected during the past few decades. We have also examined historical material from the Břešťany Clay, which is housed in the collections of the National Museum in Prague, and in the collection of the Senckenberg Museum for Mineralogy and Geology in Dresden, Germany. Both localities are situated in the Most Basin and belong among the well known Lagerstätten in Central Europe. The overlaying coal seam horizons offer unique state of preservation of fauna and flora together with opportunity to study changes of their assemblages in a short time period of development (e.g., Kvaček et al., 2004). Insect fossils are also well known counting almost 350 specimens within 11 orders (Prokop, 2003). Several species are well linked to other Neogene localities (e.g., Prokop and Nel, 2000; Fikáček et al., 2008). Individual plant tissues and organs are often found together allowing so called "Whole-plant" reconstructions (Kvaček, 2008). Exceptionally preserved parts of the plants, especially leaves, seeds, fruits and even wood, provide also very important information on prevailing climatic conditions at that time (Kvaček, 1998, 2000; Sakala, 2007).

Our research focused on an assemblage of 3509 fossil dicotyledonous leaves and 133 *Taxodium* branchlets. Twenty-three fossiliferous horizons overlying the coal seam of the Bílina Mine, together with the corresponding layers of the Břešťany Clay, are grouped into three main sedimentary environments [Clayey Superseam Horizon (CSH), Delta Sandy Horizon (DSH) and Lake Clayey Horizon (LCH) sensu Bůžek et al. (1992), Fig. 1]. These horizons contain floral assemblages of rather distinct composition and thus probably represent different ecosystems reflecting rapid palaeoenvironmental changes (Kvaček, 1998; Kvaček et al., 2004). The sediments of the Most Formation represent a coal-bearing basin fill that can be divided into four basic units: the Duchcov ("Underlying"), the Holešice ("Main Seam"), the Libkovice ("Overlying") and the Lom ("Lom Seam") members sensu Domácí (1977). The deposits of the CSH and the DSH consisting of sandy–clayey delta bodies and overlying the main lignite seam are included in the Holešice Member; the LCH deposits form the basis of the Libkovice Member. The rocks underlying the main coal seam of the Holešice Member were assigned to mammal zone MN3a, early Burdigalian (~early Eggenburgian) (Fejfar, 1989; Fejfar and Kvaček, 1993). The Libkovice Member of the Most Basin was dated by palaeomagnetically (Bucha et al., 1987); for the lower part of this member, comprising the Břešťany clays an age of 20 Ma was inferred. According to the different floral assemblages occurring in specific sedimentary environments, all three horizons represent distinct ecosystems: 1) a swamp forest, 2) a riparian–levee forest and 3) an upland lakeshore forest (Bůžek et al., 1987; Boulter et al., 1993; Sakala, 2000; Kvaček et al., 2004). However, the various types of the forest vegetation give only approximate palaeoclimatic data and the ratio of deciduous vs. evergreen

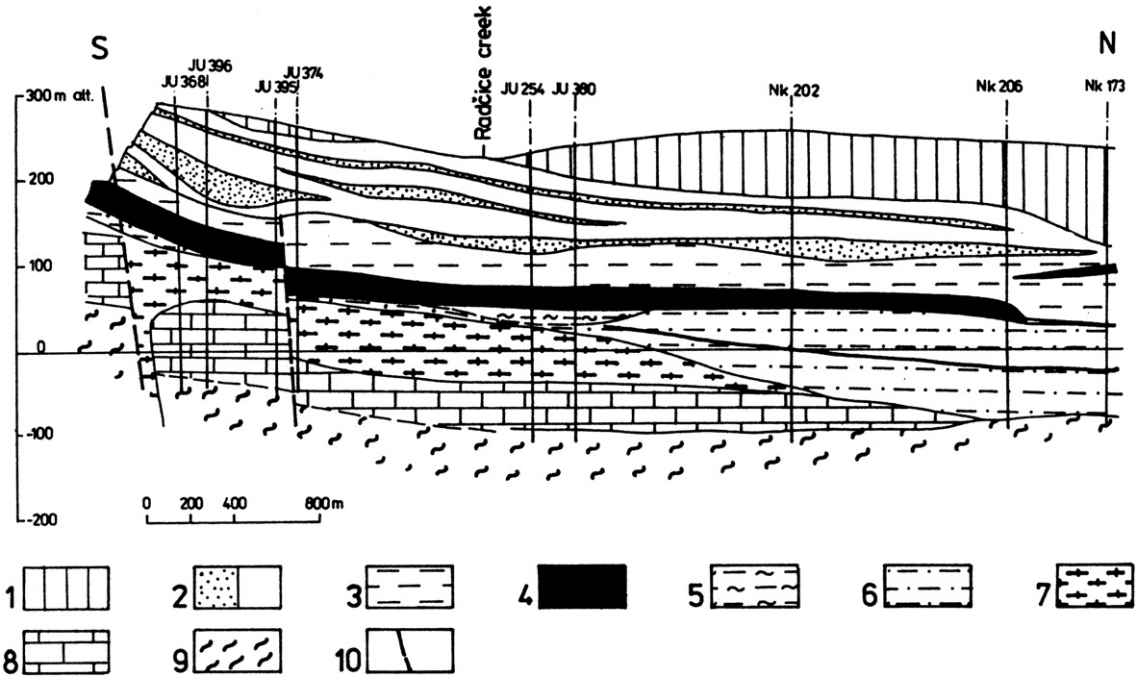



**Fig. 1.** Geological section of the Bílina Mine. (1) Lake Clayey Horizon; (2) Delta Sandy Horizon (sand, clay); (3) Clayey Superseam Horizon; (4) Coal Seam; (5) coaly clay; (6) Lower Sandy–clayey Member; (7) Neovolcanites; (8) Upper Cretaceous; (9) crystalline basement; (10) fault.
Adopted from Bůžek et al., 1992.

woody elements do not precisely indicate the variation of the palaeoclimatic conditions. The age and geological and palaeoclimatic setting of the Most Basin (in older literature often called North Bohemian Brown Coal Basin) has been briefly summarised by Kvaček (1998) and Prokop et al. (2010).

Our research involves two different approaches. The first is focused on the quantitative evaluation of galls according to environmental and ecosystem attributes. We suppose the direct influence of the climatic conditions on the frequency and diversity of galls in individual horizons as recorded from previous studies (Price et al., 1998; Cuevas-Reyes et al., 2004, 2006). In order to compare different horizons within this succession and to other localities, rarefaction curves were applied, using the rarefaction method without repetition. This procedure was done using the Vegan Package implemented in the R statistics environment (R Development Core Team, 2009). The sample size for each horizon was standardized by selecting a random subset of 50 leaves without replacement, the damage diversity (all damage types and galling damage types) for the subsample was calculated. This process was repeated 5000 times, and the results were averaged to obtain the standardized damage diversity for each floral association. The same processing was used to standardize damage diversity to 25 leaves for all taxa of which sufficient material was available. The same slightly modified procedure was for used the galling diversity rarified to the number of occurrences. Consequently, each gall was identified to distinguish distinct types of damage (Damage Types, abbrev. DTs) following the classification of Labandeira et al. (2007).

The second approach focuses on the comparative morphology of the fossil galls, the identification of their possible causers and on finding of their living relatives. We anticipate close relationship between fossil and modern gall causers according to the slow evolutionary rate of the Neogene insects' orders and families (Grimaldi and Engel, 2005). The form and the size and the position of the galls on fossil leaves were compared to galls occurring on leaves on the same or related living plant taxa, using identification keys for recent galls, e.g., Houard (1908–1909), Buhr (1964–1965), and Redfern et al. (2002). We compared fossil galls and their impressions on leaves with published illustrations or with recent galls caused by various gall-inducing organisms kept in the collection of gall midges and eriophyid mites gathered by one of us (MS).

Each leaf with fossil galls or their impressions (see Plates I, II) was photographed using a Canon D550 camera with a reverse MP-E 65 mm lens or a EF-S 60 mm lens. Original photographs were processed using the image-editing software Adobe Photoshop 8.0. We follow the systematics of Skuhravá (1986, 1989) and Gagné (2004, 2010) for the Cecidomyiidae (Diptera), and Amrine et al. (2003) for the Eriophyidae (Acari).

## 4. Results

### 4.1. Quantitative analysis

The bulk floral assemblage consists of 3509 fossil leaf impressions and is from one of the richest fossil sites in the Neogene of the Central Europe. The dataset comprises 89 plant taxa, some of them can be identified only on generic or even family level. More than 25 specimens represent thirty-nine taxa. Twenty-six show at least one type of galling damage. The total diversity of galling types in all three horizons comprises 16 distinct types with 151 separate occurrences. Preliminary work by Kvaček and Teodoridis (2007) and Prokop et al. (2010) show differences in floral composition in each horizon, representing distinct environments; this was confirmed by Knor et al. (2012). Therefore, each horizon is discussed separately; the CSH was excluded due to the lack of a sufficient number of specimens. Basic information concerning the number of the plant taxa and gall diversity in all three horizons is briefly summarised in Table 1.

#### 4.1.1. Delta Sandy Horizon

The Delta Sandy Horizon brought a wealth of plants macrofossils concentrated in many fossiliferous layers (Bůžek et al., 1992), which document a riparian forest on fertile soil consisting mostly of broad-leaved trees. The main sedimentary environment is represented by shallow pond or oxbow lake with calm water. The plant assemblage from this horizon comprises 2235 fossil leaf specimens, belonging to

82 plant taxa, of which 32 are represented by at least 25 specimens, whereas galls occur on more than half of them (18 plant taxa: Fig. 2, Table 2).

#### 4.1.2. Lake Clayey Horizon

The overlying Lake Clayey Horizon is represented by the Břešťany clays and an equivalent facies in the Bílina Mine quarry. The main sedimentary environment is characterised by deepening lake conditions. Plant assemblage of LCH is significantly less diversified than that of DSH (Table 1). This horizon also includes elements of drier slope vegetation, like *Pinus* L., 1753, *Tilia* L., 1753, *Comptonia* L'Héritier ex Aiton, 1789. Its association consists of 1260 specimens of fossil leaves, comprising 47 taxa, of which twelve are represented by 25 or more specimens. Galls are recorded from nine taxa represented. The Lake Clayey Horizon differs in many respects from the underlying Delta Sandy Horizon including the presence of galls. Individual plants taxa with at least 25 leaves and their gall diversity are introduced in Table 3.

### 4.2. Systematic part

**Order Coniferales**
**Family Cupressaceae**
**Genus *Taxodium* L. C. M. Richard, 1810**
***Taxodium dubium*** (**Sternberg**, **1823**) **Heer**, **1855**

*Taxodium dubium* differs only slightly in most *morphological* and ecological aspects from recent species of this genus, which are distributed in lowland swamp forests of the southeastern United States (*Taxodium distichum* (L.) Richard, 1810) and Mexico (*T. mucronatum* Tenore, 1854) (Kvaček, 1976). Sterile twigs have flattened, distichously arranged needles, which alternate at unequal distances. Needles have an acute apex and their base is often very shortly petiolate and obtuse; the venation is characterised by a strong and distinct midrib (Teodoridis, 2001).

Collection numbers of the fossil material: DB1-119 (Plate I. 1, 2), DB5-140, DB76-106, G-1661

Description: All specimens consist of short branchlets, 50–60 mm long. A large number of dark, carbonised, globular, 0.47–0.76 mm large corpuscles are recognisable on the needles. They are similar in shape, size and distribution to galls caused by recent gall midge species of the genus *Taxodiomyia* Gagne, 1968 (Diptera: Cecidomyiidae) (Plate I. 3). The exact identification is not available yet and will be dealt with in a future paper on all cecidomyid galls on *Taxodium* (Gagné, pers. comm.). In North America, more species of Cecidomyiidae occur on Cupressaceae. Their galls are found on needles of *T. distichum*, e.g., *Itonida taxodii* Felt, 1911 and *I. anthici* Felt 1913. These two species induce galls showing a different morphotype, clearly distinguishable from the fossil ones described above. The cypress twig gall midge *Taxodiomyia cupressiananassa* Osten Sacken, 1878 attacks the bald cypress (*T. distichum*) and the pond cypress (*T. distichum* var. *imbricatum* (Nuttall, 1818) Croom, 1837), inducing galls that develop from leaf buds. The morphology of these galls is reminiscent to those caused by *Adelges abietis* (L., 1758) (Hemiptera: Adelgidae) occurring on spruce twigs.

Comments: The extant North American gall midge *Sequoiomyia taxodii* Felt, 1916 recorded on *T. distichum* causing swollen aborted seeds is also known from the Pleistocene of Washington D.C. (USA) (Berry, 1923). Lewis et al. (1990) refer about the species of fossil *Thecodiplosis* Kieffer, 1895 (Diptera: Cecidomyiidae) on *Taxodium* from Miocene deposits of Northern Idaho, USA.

**Order Laurales**
**Family Lauraceae**
**Genus *Daphnogene* Unger**, **1845**
***Daphnogene polymorpha*** (**A. Braun**, **1845**) **Ettingshausen**, **1851**

This evergreen tree or shrub was a characteristic component of subtropical forests in the elevated parts of basin. The morphology of the fruits indicates a close relationship with *Cinnamomum camphora* (L.) J. Presl 1825 from subtropical and tropical Asia (Kvaček and Walther, 1974). Leaves are elliptic to ovate, tri-veined, 50–60 (70) mm long and 20–30 mm broad, with a cuneate base, an attenuate to acute apex and an entire margin (Teodoridis, 2001). All affected leaves show the presence of one type of identifiable gall.

Collection numbers of fossil material: G-1819, G-1822, G-1836, G-1837, G-5451, G-5453 (Plate I. 4), G-9150, DB32-286, DB11-105

Description: Fossil leaves 55–70 mm long and about 25 mm broad, with many small, round, nodular formations, 0.5–2 mm in diameter, on leaf blade following the trajectories of the main and lateral veins, sometimes also in the area between them. These formations are almost identical to galls found by Ambrus and Hably (1979) on *Daphogene bilinica* (Unger) Knobloch et Kvaček, 1967 from the upper Oligocene of Baromállás, Hungary, that were assigned to the eriophyid mite *Eriophyes daphnogene* Ambrus et Hably, 1979 (Acari: Eriophyidae).

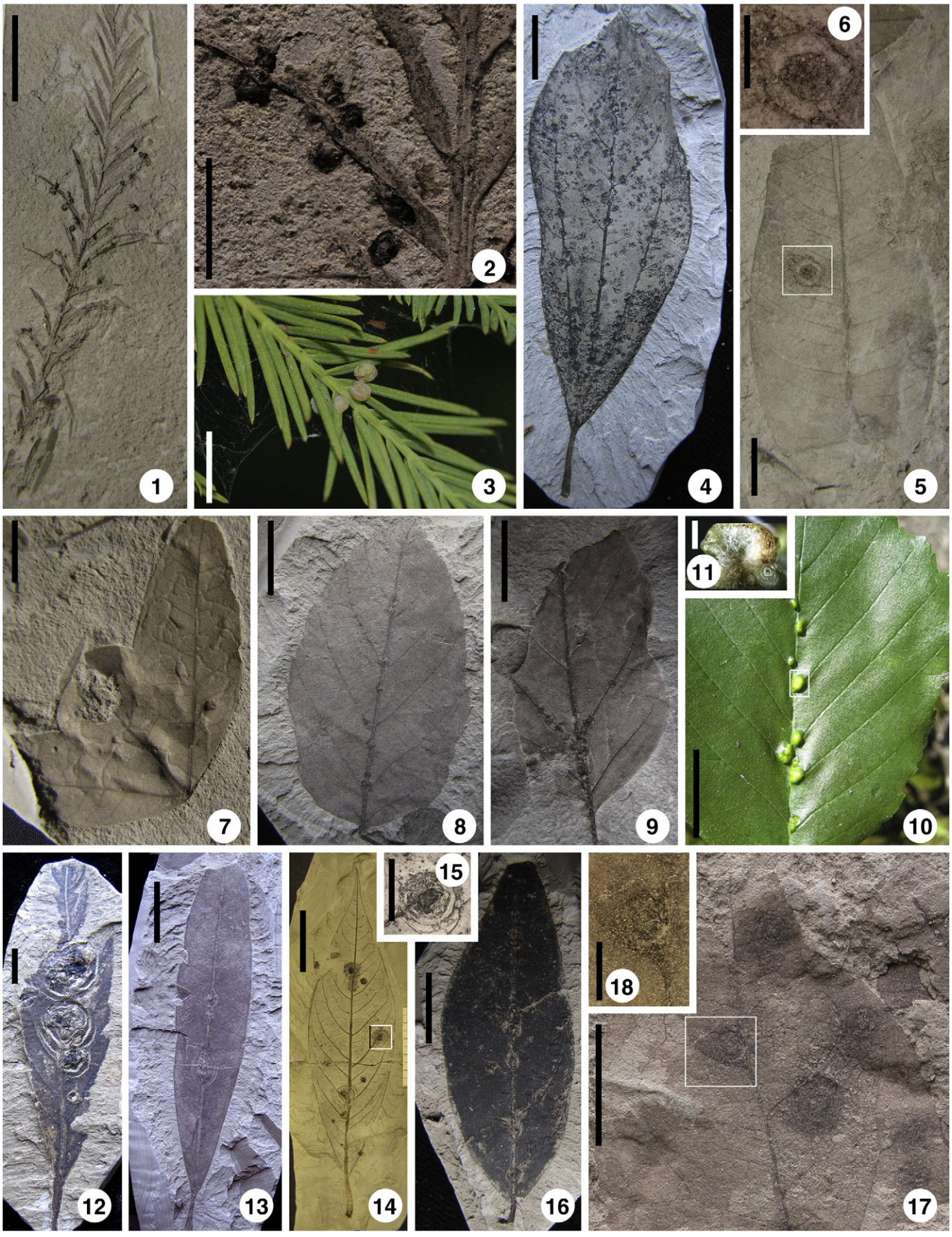
**Order Myrtales**
**Family Lythraceae**
**Genus *Decodon* Gmelin 1791**
***Decodon gibbosus*** (**E. M. Reid**) **E. M. Reid 1929** (="***Ficus*" *multinervis* Heer**, **1856**)

*Decodon gibbosus* was probably a low shrub growing in shallow water in the *Taxodium* swamp forests as can be assumed on the basis of the habitus of its nearest living relative *Decodon verticillatus* (L.) Elliot, 1821 from eastern North America (Kvaček and Sakala, 1999). The leaves are entire-margined, linear to broadly lanceolate, 100–250 mm long and 15–55 mm broad, cuneate to long cuneate with long petioles (Teodoridis, 2001). Only a single specimen bears a unique type of gall.

Collection number of the fossil specimen: DB2-111 (Plate I. 5, 6)

Description: Fossil leaf, 63 mm long and 31 mm broad, with small round formations showing an inner dark circle of 2.5 mm in diameter, surrounded by a pale-coloured circle and an outer darker circle of 5 mm in diameter. The inner circle consists of approximately twenty separate rounded convex cups, especially along its circumference. Similar galls are caused by the recent gall midge *Horidiplosis ficifolii* Harris, 2003 (Diptera: Cecidomyiidae) on leaves of *Ficus benjamina* L.,

**Plate I.** Arthropod galls on selected plant taxa from the Bílina mine (Most Basin, Czech Republic). (1) Branchlet of *Taxodium dubium* (Cupressaceae) with several cecidomyid galls (Diptera: Cecidomiidae) (DB1-119); (2) detailed photo of galls on *Taxodium dubium* (Cupressaceae) (DB1-119); (3) branchlet of *Taxodium distichum* with galls caused by gall midge *Taxodiomyia* sp. (Cecidomyiidae); (4) small galls caused by *Eriophyes daphnogene* on *Daphnogene polymorpha* (Lauraceae) (G-5453); (5) leaf of *Decodon gibbosus* (Lythraceae) with a large circular gall caused by a gall midge (Cecidomyiidae); (6) enlarged view of the gall on *Decodon gibbosus* (DB2-111); (7) small cecidomyid gall on the leaf of *Podocarpium podocarpum* (Fabaceae) (DB57-299); (8) galls of eriophyoid mites (Acari: Eriophyoidea) on the midrib of *Alnus julianiformis* (Betulaceae) (G-1680); (9) slightly morphologically different type of galls of eriophyoid mites (Acari: Eriophyoidea) on primary and secondary veins of *Alnus julianiformis* (G-1785); (10) galls of *Eriophyes inangulis* on a leaf of *Alnus glutinosa*; (11) detail of the eriophyoid gall on *Alnus glutinosa*; (12) large cynipid galls (Hymenoptera: Cynipidae) on *Quercus rhenana* (Fagaceae) (G-7647); (13) galls with less prominent circular edges on the midrib of the other leaf of *Quercus rhenana* (G-3972); (14) leaf of *Quercus rhenana* with galls, probably of cynipid origin, on primary and secondary veins (Bn-985); (15) enlarged view of cynipid gall on *Quercus rhenana* (Bn-985); (16) small, rounded, probably eriophyoid galls on a leaf of *Trigonobalanopsis rhamnoides* (Fagaceae) (G-9329) (17) Leaf of *Carya serrifolia* (Juglandaceae) with four circular galls caused by *Phylloxera* sp. (Hemiptera: Phylloxeridae) (ZDI0021), (18) Enlarged view of the gall on *Carya serrifolia* (ZDI0021). Panels 13, 14 — scale bar = 40 mm; panels 1, 4, 5 7–11, 16, 17 — scale bar = 10 mm; panel 3 — scale bar = 5 mm; panels 2, 6, 15, 18 — 3 mm, panel 11 — scale bar = 1 mm.



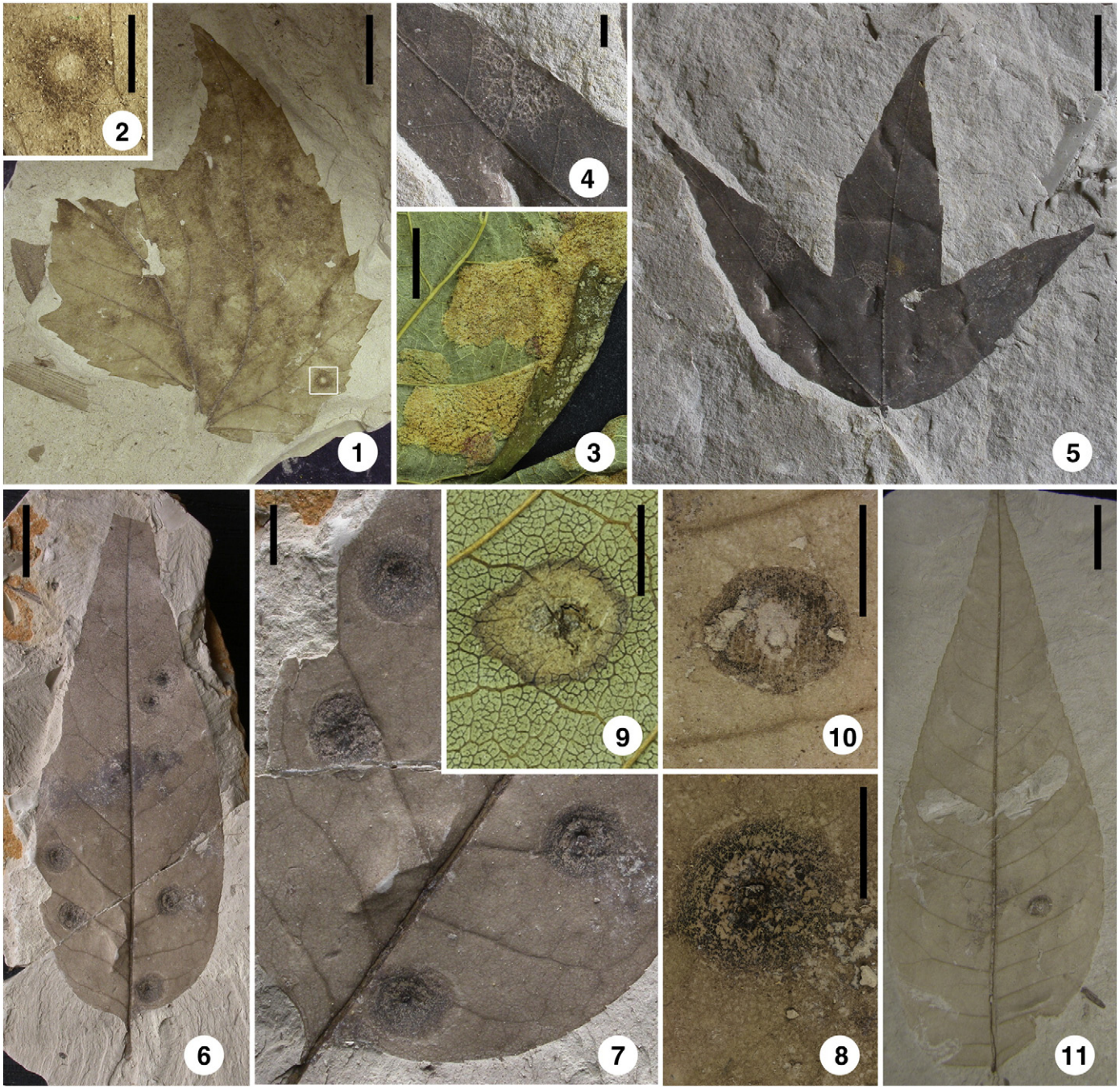



**Plate II.** Arthropod galls on selected plant taxa from the Bílina mine (Most Basin, Czech Republic). (1) Leaf of *Tilia brabenecii* (Tiliaceae) with cecidomyid galls (*Physemocecis* sp., Diptera: Cecidomyiidae) (DB36-156); (2) Detail of the gall on *Tilia brabenecii* (DB36-156); (3) Detailed view on erineum of *Aceria pseudoplatani* (Acari: Eriophyidae) on a leaf of *Acer pseudoplatanus*; (4) Galls possibly caused by *Aceria* sp. on a leaf of *Acer angustilobum*, (ZDI048); (5) Leaf of *Acer angustilobum*, erinea irregularly dispersed over the leaf blade (ZDI048); (6) Leaf of *Fraxinus bilinica* with galls caused by *Dasineura* sp. (Diptera: Cecidomyiidae) (ZDI023); (7) Detail of the galls on *Fraxinus bilinica* caused by *Dasineura* sp. (Cecidomyiidae) (ZDI023); (8) Enlarged view on the cecidomyid gall on *Fraxinus bilinica* (ZDI023); (9) Enlarged view of the gall of *Dasineura fraxinea* (Cecidomyiidae) on *Fraxinus excelsior*; (10) Enlarged view on the cecidomyid gall (Cecidomyiidae) on *Fraxinus bilinica* (ZDI045); (11) Leaf blade of *Fraxinus bilinica*, with a solitary gall visible on the right side of the midrib (ZDI045). Panels 1, 5, 6, 11 — scale bar = 10 mm; panels 2, 3, 4, 7–10 — scale bar = 3 mm.

1767 occurring in China and also recently imported into Europe (the Netherlands and the Czech Republic).

**Order Fabales**
**Family Fabaceae**
**Genus *Podocarpium* A. Braun ex Stizenberger, 1851**
***Podocarpium podocarpum* (A. Braun, 1851) Herendeen, 1992**

This species is only distantly related to some members of the Amherstieae and Detarieae from tropical Africa (Herendeen, 1992). It was probably a thermophilous and xerophilous shrub or tree, preferring elevated sites of browncoal basin (Bůžek et al., 1996). It is apparently a Paleogene–Neogene Eurasian element that has not yet been found in North America (Herendeen, 1992). Leaflets are oval, 15–25 mm long and 8–10 mm broad with an acute apex, an entire margin, a strong, straight midrib and one camptomodromous basal vein (Teodoridis, 2001).

Collection number of fossil specimen: DB57-299 (Plate I. 7)

Description: Fossil leaflet of about 45 mm long, with a small dark, three-dimensional, ovoid, concave, slightly irregular, 2.3 × 1.7 mm

**Table 1**
All three horizons at Bílina Mine locality — all plant taxa, proportionality of the galls and gall diversity.

| Horizon | Taxa[a] | Leaves | Taxa rarefied to 1000 leaves | Total galls | Galls per one leaf | Gall diversity rarefied to | |
|---|---|---|---|---|---|---|---|
| | | | | | | 1000 leaves | 20 occurrences |
| LCH | 46 | 1260 | 44.66 | 88 | 0.067 | 9.843 | 5.033 |
| DSH | 81 | 2233 | 75.06 | 61 | 0.027 | 9.907 | 8.637 |
| CSH[b] | 10 | 16 | n/a | 2 | 0.125 | n/a | n/a |

[a] All plant taxa occurring in the site, including those represented by less than 25 specimens.
[b] This horizon was excluded from comparison due to the lack of the sufficient number of specimens.

large formation on the leaflet blade. Its morphology corresponds to some special types of galls, i.e. blister galls, induced by many kinds of galling insects (psyllids, cecidomyids), mites and also fungi. Due to the lack of close relative taxa the exact identification of the causer remains impossible, although the fossil formations are very similar to blister galls caused by the extant gall midge *Meunieriella aquilonia* Gagné, 1984 (Diptera: Cecidomyiidae) on *Gleditsia triacanthos* L., 1753 in North America (Gagné, 1989, fig. 287, p. 189).

**Order Fagales**
**Family Betulaceae**
**Genus *Alnus* Miller, 1754**
***Alnus julianiformis* (Sternberg, 1823) Kvaček et Holý 1974**

This species is one of the most common deciduous trees in our collection. In fact, it is the most important taxon in floodplain and swamp forest ecosystems. It shows a very close affinity to extant species of *Alnus* from central China, e.g., *A. trabeculosa* Handel-Mazzetti 1922 (Kvaček and Holý, 1974). Leaves of this tree are found in large amounts in all horizons. Leaves are elliptic, 45–55 mm long and 28–39 mm broad, with a short acute apex and a cuneate base. Leaves are entire-margined in the basal part, and then become simple-serrate with acute teeth. Many show plant–insect interactions, especially galling.

Collection numbers of fossil material: G-1680 (Plate I. 8), G-3218 G-1698 G-1764, G-1785 (Plate I. 9), G-2141 G-3258 G-3309, G-5356, G-9214

Description: All affected fossil leafs have three-dimensional, rounded spots with prominent borders and a central depression. These are 1.5–2 mm in diameter, seldom 4 mm, and situated on the primary vein, occasionally on the secondary veins. The size, the morphology and the distribution of these formations are very similar to galls caused by the recent eriophyid mite *Eriophyes inangulis* (Nalepa, 1919) (Acari: Eriophyidae) that in Europe occurs abundantly on modern *Alnus glutinosa* (L.) Gaertner, 1791 and *A. incana* (L.) Moench, 1794. Especially the size and distribution of the galls, associated with above mentioned host plants, allows us to assign them to *Eriophyes* Siebold, 1851.

Comments: Cockerell (1927) mentioned *Eriophyes laevis* from the upper Miocene of Bridge Creek, Oregon, U.SA. Straus (1977) reported the mite *Eriophyes* (*Aceria*) *inangulis* from the Pliocene of Willershausen, Germany.

**Family Fagaceae**
**Genus *Quercus* L. 1753**
***Quercus rhenana* (Kräusel et Weyland, 1950) Knobloch et Kvaček, 1976**

*Quercus rhenana* was a thermophilous and evergreen tree with long lanceolate, entire-margined leaves, growing on drier places of

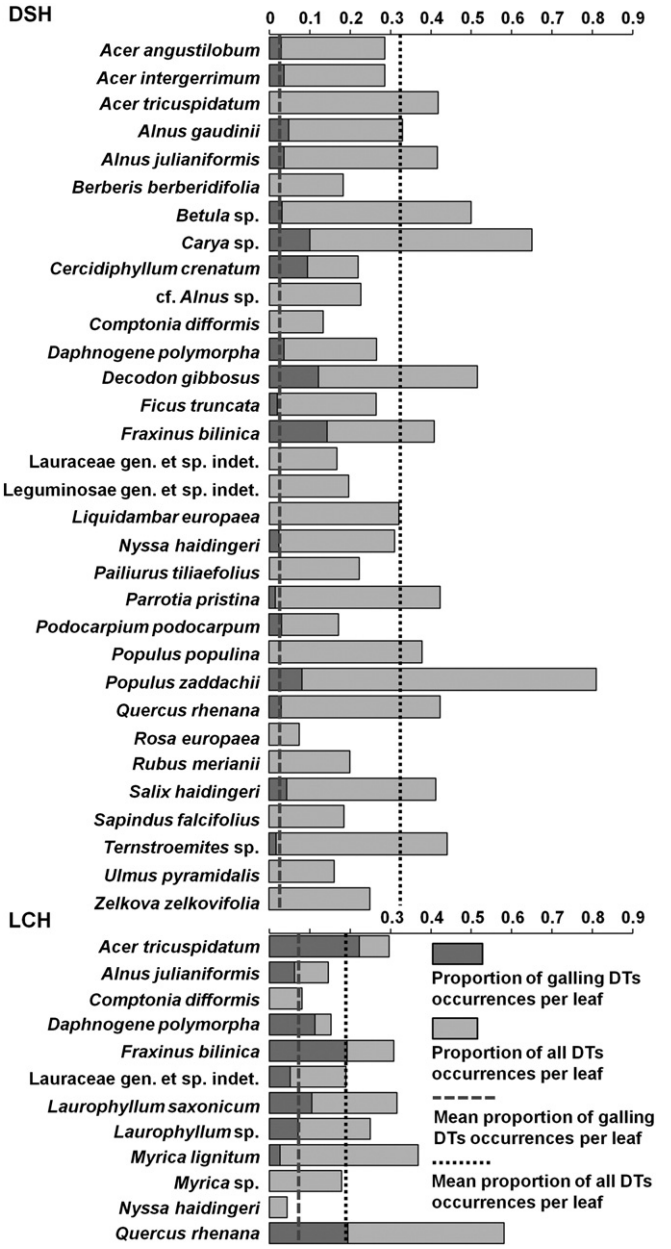



**Fig. 2.** Relation between proportions of all damage occurrences per one leaf and the galling occurrences per one leaf in case of the most abundant genera (N≥25 specimens) in DSH and LCH assemblages.

the brown-coal basin; its closest extant relative in the North America is *Q. virginiana* P. Miller, 1768 (Knobloch and Kvaček, 1976).

Collection number of the fossil material: G-3972 (Plate I. 13), G-7647 (Plate I. 12)

Description: The first leaf is very narrow, 220 mm long and 50 mm broad, the second one is shorter, 100 mm long and 30 mm broad. Both have large formations on the main vein, very variable in size, following each other, filled up with concentric fragmentary circles, created by pressure of overlying layers when the great former three-dimensional galls collapsed. Affections on the first leaf are all elongated in the direction of midvein. The biggest is 22 mm in diameter, and two smaller formations, 9 mm and 8 mm in diameters, all in the center showing complicated structures. In case of the second leaf, we can observe four affections (15, 13, 6.8, 1.7 mm in diameter), not so elongated, rather more circular, with the above-mentioned inner complicated structure less expressed, but undoubtedly of the same

**Table 2**
DSH plant taxa with at least 25 specimens together with their gall diversity and DTs' composition.

| Taxon ≥ 25 specimens | Leaves | Galls (DTs'[a] No.) | Total gall diversity | Total gall occurrences | Gall diversity rarefied to | |
|---|---|---|---|---|---|---|
| | | | | | 25 leaves | three occurrences |
| *Acer angustilobum* | 35 | 32 | 1 | 1 | 0.514 | n/a |
| *Acer intergerrimum* | 28 | 32 | 1 | 1 | 0.582 | n/a |
| *Acer tricuspidatum* | 91 | – | 0 | 0 | 0 | 0 |
| *Alnus gaudinii* | 85 | 33, 85, 145, 153 | 4 | 4 | 0.976 | 3 |
| *Alnus julianiformis* | 166 | 11, 33, 110 | 3 | 6 | 0.742 | 2.25 |
| *Berberis berberidifolia* | 55 | – | 0 | 0 | 0 | 0 |
| *Betula* sp. | 32 | 11 | 1 | 1 | 0.564 | n/a |
| *Carya* sp. | 60 | 11, 32, 110, 145, 163 | 5 | 6 | 1.926 | 2.8 |
| *Cercidiphyllum crenatum* | 32 | 11, 33 | 2 | 3 | 1.338 | 2 |
| cf. *Alnus* sp. | 31 | – | 0 | 0 | 0 | 0 |
| *Comptonia difformis* | 45 | – | 0 | 0 | 0 | 0 |
| *Daphnogene polymorpha* | 83 | 32, 80 | 2 | 3 | 0.728 | 2 |
| *Decodon gibbosus* | 33 | 33, 49, 110 | 3 | 4 | 1.890 | 2.5 |
| *Ficus truncata* | 53 | 32 | 1 | 1 | 0.392 | n/a |
| *Fraxinus bilinica* | 49 | 11, 32, 34, 80, 144 | 5 | 7 | 2.590 | 2.714 |
| Lauraceae gen. et sp. indet. | 78 | – | 0 | 0 | 0 | 0 |
| Leguminosae gen. et sp. indet. | 51 | – | 0 | 0 | 0 | 0 |
| *Liquidambar europaea* | 53 | – | 0 | 0 | 0 | 0 |
| *Nyssa haidingeri* | 87 | 11, 34 | 2 | 2 | 0.498 | n/a |
| *Pailiurus tiliaefolius* | 36 | – | 0 | 0 | 0 | 0 |
| *Parrotia pristina* | 66 | 11 | 1 | 1 | 0.306 | n/a |
| *Podocarpium podocarpum* | 64 | 33 | 1 | 2 | 0.540 | n/a |
| *Populus populina* | 29 | – | 0 | 0 | 0 | 0 |
| *Populus zaddachii* | 37 | 11, 33, 163 | 3 | 3 | 1.502 | 3 |
| *Quercus rhenana* | 33 | 32 | 1 | 1 | 0.558 | n/a |
| *Rosa europaea* | 27 | – | 0 | 0 | 0 | 0 |
| *Rubus merianii* | 25 | – | 0 | 0 | 0 | 0 |
| *Salix haidingeri* | 46 | 11, 80 | 2 | 2 | 0.772 | n/a |
| *Sapindus falcifolius* | 27 | – | 0 | 0 | 0 | 0 |
| *Ternstroemites* sp. | 59 | 145 | 1 | 1 | 0.336 | n/a |
| *Ulmus pyramidalis* | 118 | – | 0 | 0 | 0 | 0 |
| *Zelkova zelkovifolia* | 56 | – | 0 | 0 | 0 | 0 |
| Total | 1770 | 11, 32, 33, 34, 49, 62, 80, 85, 110, 144, 145, 153, 163 | 13[b] | 49 | – | – |

[a] Damage types. From Labandeira et al. (2007) and subsequent additions in preparation.
[b] The same total diversity as in the case of all taxa (including those with less than 25 specimens).

type. A very similar gall was found also on the specimen Bn-985 (Plate I. 14, 15) from collection of Museum for mineralogy and geology in Dresden, which is however not involved in quantitative evaluation. These Fossil formations are very similar to galls caused by the recent species of gall wasp *Cynips quercusfolii* Linnaeus, 1758 (Hymenoptera: Cynipidae) on leaves of *Quercus robur* P. Miller, 1768 and *Q. petraea* Lieblein, 1784, which may reach a size from 10 to 20 mm (Buhr, 1964–1965, Taf. 16: 255, 256). An almost identical pattern according the size, shape and distribution can be seen in galls of cecidomyid species *Dryophanta polita* Bassett, 1881 on *Quercus minor* Sargent, 1889 in North America.

### Genus *Trigonobalanopsis* Kvaček et Walther, 1988
### *Trigonobalanopsis rhamnoides* (Rössmässler, 1840) Kvaček et Walther, 1988

Genus *Trigonobalanopsis*, an extinct evergreen member of the family Fagaceae was especially abundant during the Neogene's warmer periods. This tree preferred acid soils of drier slopes. It is considered as European endemic, as far as it can be judged from its occurrence. Similarly, distantly related recent tree *Formanodendron doichangensis* (A. Camus) Nixon et Crepet, 1989 grows in mountain forests of Laos and South China (Nixon and Crepet, 1989).

**Table 3**
LCH plant taxa with at least 25 specimens together with their gall diversity and DTs' composition.

| Taxon ≥ 25 specimens | Leaves | Galls (DTs'[a] No.) | Total gall diversity | Total gall occurrences | Gall diversity rarefied to | |
|---|---|---|---|---|---|---|
| | | | | | 25 leaves | Three occurrences |
| *Acer tricuspidatum* | 27 | 33, 215 | 2 | 6 | 1.600 | 1.5 |
| *Alnus julianiformis* | 289 | 32, 33, 34, 110 | 4 | 18 | 1.146 | 1.939 |
| *Comptonia difformis* | 25 | – | 0 | 0 | 0 | 0 |
| *Daphnogene polymorpha* | 224 | 32, 33, 110 | 3 | 25 | 1.542 | 1.866 |
| *Fraxinus bilinica* | 26 | 32, 33, 84 | 3 | 5 | 2.194 | 2.2 |
| Lauraceae gen. et sp. indet. | 175 | 32, 33, 49 | 3 | 9 | 0.992 | 2.095 |
| *Laurophyllum saxonicum* | 38 | 32, 33, 34 | 3 | 4 | 1.758 | 2.5 |
| *Laurophyllum* sp. | 84 | 32, 33, 117, 145 | 4 | 6 | 1.410 | 2.45 |
| *Myrica lignitum* | 38 | 11 | 1 | 1 | 0.506 | n/a |
| *Myrica* sp. | 56 | – | 0 | 0 | 0 | 0 |
| *Nyssa haidingeri* | 46 | – | 0 | 0 | 0 | 0 |
| *Quercus rhenana* | 31 | 33, 34, 84 | 3 | 6 | 2.268 | 2.25 |
| Total | 1059 | 11, 32, 33, 34, 49, 84, 110, 117, 145, 153, 215 | 11[b] | 80 | – | – |

[a] Damage types. From Labandeira et al. (2007) and subsequent additions in preparation.
[b] The same total diversity as in the case of all taxa (including those with less than 25 specimens).

Number of fossil material: G-9329 (Plate I. 16)

Description: Leaf is elliptic to obovate, 47.6 mm long and 19 mm broad with missing apex, obviously acute or attenuate, entire margin and brochidodromous venation. Midrib is strong, straight, secondary veins are thin, alternate, regularly spaced, and tertiary veins are straight or forked. Several three-dimensional circular or oval swollen formations with shallow depressions around are situated mostly on primary and also on secondary veins. All of these galls show superficial resemblance with those on *Alnus julianiformis* (Sternberg) Kvaček et Holý, 1974 and *Daphnogene polymorpha* (A. Braun) Ettingshausen, 1851 caused by mites of genus *Eriophyes* Siebold, 1851. Given the lack of the nearest living relatives of *Trigonobalanopsis rhamnoides*, it is difficult to make a closer taxonomic determination of the galls based purely on their morphology.

**Family Juglandaceae**
**Genus *Carya* Nuttall, 1818**
***Carya serrifolia* (Goeppert, 1855) Kräusel, 1921**

Today, the genus *Carya* occurs in North America and East Asia, exhibiting a typical disjunct distribution. *Carya serrifolia* is a typical member of the floodplain forest plant assemblage, like now in eastern North America (Bůžek, 1971). The nearest living relative of this species is *Carya poilanei* (Chevalier) Leroy, 1950 from East Asia, which shows a similar fruit morphology (Czaja, 2003). Leaflets are usually oblong, elliptic to ovate, 45–100 mm long and 20–40 mm broad, with a cuneate base, an acute apex and a finely serrated margin (Teodoridis, 2001).

Collection number of the fossil material: ZDI0021 (Plate I. 17, 18), DB32-285

Description: Two leaflets, both about 65 mm long and 25 mm broad, show the presence of small circular concave, sometimes multilocular, 0.5–1.5 mm large formations. These fossil impressions are very similar to galls caused by the recent gall midge *Caryadiplosis biconvexa* Gagné, 2008 (Diptera: Cecidomyiidae) on *Carya* spp. occurring in North America (Gagné, 2008, p.120, figs 167–168). However, there are other species forming similar galls on leaves of North American hickories. Apart from the species mentioned above, there are many species of the genus *Caryomyia* Felt, 1909 from the same family Cecidomyiidae producing similar galls. A very similar morphology is caused by *Phylloxera caryaeglobuli* Walsh, 1863 (Hemiptera: Phylloxeridae), which is in our opinion a more likely candidate than the members of both genera from the family Cecidomyiidae. The only difference is the slightly smaller size of the affections, but they show nearly the same distributional pattern and superficial appearance.

Comments: Straus (1977) described the galls of eriophyid mite *Aceria erinea* Nalepa, 1891 forma *caryae-pterocaryae* from the upper Pliocene of Willershausen, Germany.

**Order Malvales**
**Family Tiliaceae**
**Genus *Tilia* L., 1753**
***Tilia brabenecii* Kvaček et Bůžek, 1994**

Most of these trees were growing on drier places, far from the sedimentary environment of the swamp basin. Consequently, in most cases, the fossil leaves were transported by the water. Its closest living relatives can be found among the species known from Caucasus and East Asia (China) (Bůžek and Kvaček, 1994). Leaves are ovate with a simple serrated margin, an obtuse apex and a strong midrib (Teodoridis, 2001).

Collection number of the fossil specimen: DB36-156 (Plate II. 1, 2)

Description: Fossil leaf, 70 mm long and 50 mm broad, with rounded spots on the leaf blade, about 3 mm in diameter, each of them consisting of an inner lighter coloured circle surrounded by a darker ring. These formations are very similar to recent galls caused by the gall midge *Physemocecis hartigi* Liebel, 1892 (Diptera: Cecidomyiidae) on leaves of *Tilia platyphyllos* Scopoli, 1771 and *T. cordata* Miller, 1768. Galls of this gall midge could be found frequently in Europe (pers. obs. Skuhrava).

Comments: Straus (1977) mentioned two species of eriophyid mites as gall inducers on leaves of *Tilia* sp., — *Eriophyes lateannulatus* Schulze 1918 and *E. exilis* Nalepa 1891 from the upper Pliocene of Willershausen, Germany.

**Order Sapindales**
**Family Sapindaceae**
**Genus *Acer* L., 1753**
***Acer angustilobum* Heer, 1859 (=*A. dasycarpoides* Heer, 1859)**

This deciduous tree was a characteristic element in the riparian and swamp forest. Its nearest living relatives are found in East Asia, e.g., *Acer ginnala* Maximowicz, 1856 that has a very similar leaf morphology (Walther, 1972; Procházka and Bůžek, 1975). We have studied 35 leaves of this species and two show identifiable galls. Both leaves are palmate, trilobed with a distinct cordate base and broadly cuneate, similarly sized lobes, oblong to oblong–lanceolate with acute apices, rounded sinuses, widely open, and with serrate margin with relatively long simple teeth.

Collection number of the fossil material: ZDI048 (Plate II. 4, 5)

Description: Fossil leaf, 74 mm long, 86 mm broad with pointed lobes, and two irregularly oval, furrowed spots of about of $6.3 \times 4.2$ mm and $10 \times 6$ mm on the leaf blade near the midvein. Both traces remind of erineum, i.e. a patch of hairs, induced by *Aceria pseudoplatani* Corti, 1905 (Acari: Eriophyidae), an extant species being common in Europe on *Acer pseudoplatanus* L. 1753 (Fig. 3.2). In North America, there is another species of eriophyid mite, *Aceria elongatus* Hodgkiss, 1913, causes an erinea of on *Acer saccharum* Marshall, 1785, showing almost the same morphology, although they are different in colour. A large variety of erinea is found on numerous taxa *Acer* L. The great similarity between different erinea of distinct species of the genus *Aceria* Kiefer, 1944 can be observed in the Holarctic region, e.g., in Europe, *Aceria eriobius* Nalepa, 1922 initiates the typical erineum showing the characteristic morphology on *Acer campestre* L., 1753 and very similar erinea, apparently induced by different species *A. psilomerus* Nalepa, 1922 on *Acer pseudoplatanus* L. Therefore, it is not possible to identify the exact causer, but it is most likely a species of *Aceria*.

Collection number of the fossil specimen: G-2264

Description: Incomplete fossil leaf, showing an irregular distribution of three-dimensional nodules of different sizes, associated with the primary and secondary veins. The nodules are irregular in shape and their size varies from approximately 0.5–2.2 mm in diameter. The galling pattern, morphology, and size are well comparable to that caused by the recent eriophyid mite *Aceria macrochela* Nalepa, 1891 (Acari: Eriophyidae) on leaves of *Acer campestre* and some other related species of *Acer*. However, the galls of common recent species whose occurrence is restricted to Europe are similar to others of the same genus. Comments: Fossil impressions probably caused by the eriophyid mite *Aceria macrochelus* are known also from upper Pliocene of Willershausen, Germany (Strauss, 1977).

**Order Lamiales**
**Family Oleaceae**
**Genus *Fraxinus* L., 1753**
***Fraxinus bilinica* (Unger, 1847) Kvaček et Hurník, 2000**

This deciduous tree was the typical element of the floodplain forest. Closely related species occur in the same type of habitat in Atlantic part of the North America (for instance *F. pennsylvanica* Marschall, 1785) and in eastern Eurasia until today (Knobloch and Kvaček, 1976; Kvaček and Hurník, 2000). Leaflets are elliptic or ovate, 50–95 mm long and 25–40 mm broad, with an acute apex, a round base and regularly serrated margins (Teodoridis, 2001).

Collection number of the fossil specimen: ZDI004

Description: The two fossil leaflets are respectively 87 mm long and 33 mm wide and 101 mm long and 39 mm broad. More than two thirds of the leaf blade is preserved of the larger specimen. Both leaflets show small, rounded, formations on the surface being 2.9–3.6 mm in diameter, surrounded by irregular spots with a rough structure.

The formations are similar to the rounded or pointed tubercles caused by recent eriophyid mites, *Aceria fraxinicola* Nalepa, 1890 (Acari: Eriophyidae), on *Fraxinus excelsior* L., 1753. However, the fossil galls are flattened because they were strongly compressed. Galls of *Aceria fraxinicola* occur abundantly in Europe.

Deformations along the main veins of the leaflets in the form of irregular swellings or tubers on the leaflet blade (ZDI004) are similar to those caused by the recent eriophyid mite *Aculus epiphyllus* Nalepa, 1892 (Acari: Eriophyidae) on *Fraxinus excelsior*. Galls of *Aculus epiphyllus* are rare in Europe.

Collection numbers of the fossil material: ZDI023 (Plate II. 6, 7), ZDI045 (Plate II. 10, 11).

Note: ZDI023 consists of part and counterpart. Of this specimen only a half of the blade is preserved, whereas ZD0145 is an almost complete leaflet. This latter leaflet is the only specimen with only one type of gall between two secondary veins.

Description: Fossil leaflets, respectively 76 mm long and 27 mm broad and 93 mm long and 35 mm broad, with seven circular three-dimensional formations, 2.5–4.5 mm in diameter on the leaf blade situated between two lateral veins, each formation with dark inner circle. The morphology, size and distribution of these formations are very similar to galls caused by the recent gall midge *Dasineura fraxinea* Kieffer, 1907 (Diptera: Cecidomyiidae) on leaflets of *Fraxinus excelsior* L. (Fig. 3.8). This type of galls is now frequent in Europe (Skuhravá and Skuhravý, 1992).

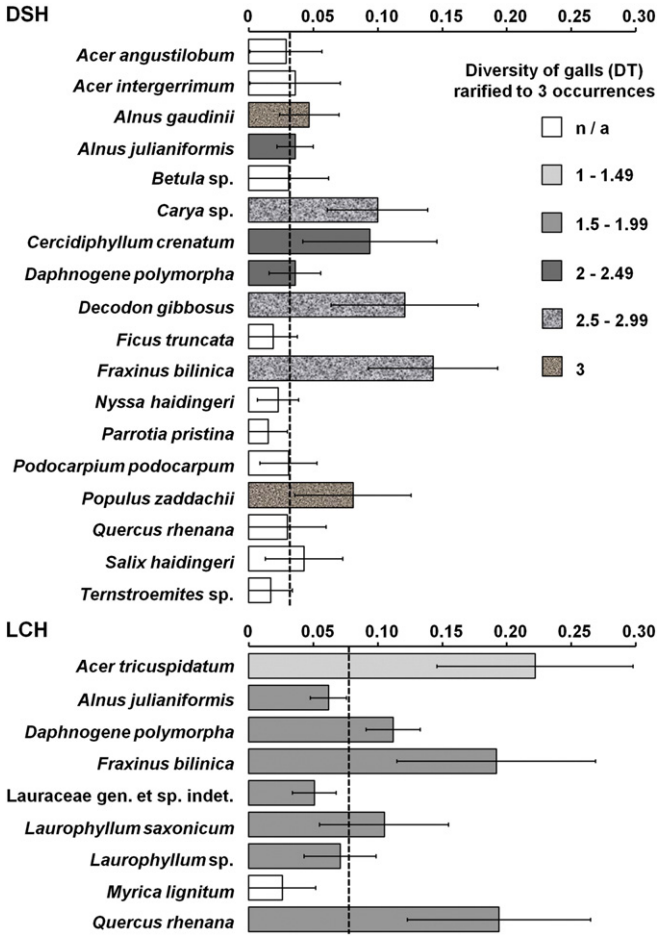



**Fig. 3.** Comparison between proportions of gall occurrences per one leaf between both horizons. Colour of the bar indicates attained galling diversity rarefied to the three galling occurrences. Error bars indicate standard error of the mean.

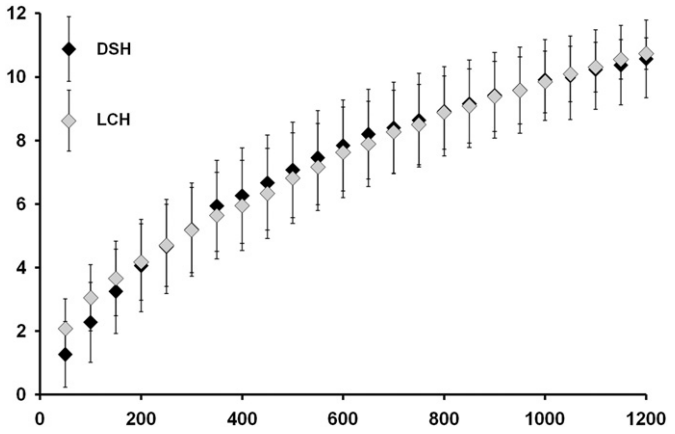



**Fig. 4.** Rarefaction curves — diversity of galling damage types rarefied to the number of leaves. Error bars indicate standard error of the mean.

## 5. Evaluation of results and discussion

### 5.1. Quantitative analysis

Frequency and particularly the diversity of galling arthropods and their activity are both strongly influenced by environmental conditions of the locality of current ecosystems (Price et al., 1998; Gonçalves-Alvim and Fernandes, 2001; Cuevas-Reyes et al., 2006). The highest taxonomic richness of galling-inducing taxa can be seen at intermediate latitudes with arid and semiarid climatic conditions of Mediterranean type characterised by sclerophyllous vegetation (Fernandes and Price, 1988, 1991; Wright and Samways, 1998), although many more further factors, such as the soil fertility via plant host diversity and composition are involved (Cuevas-Reyes et al., 2003; Veldtman and McGeoch, 2003).

The quantitative analysis of the galling incidence on fossil dicotyledonous leaves from the LCH and the DSH from the Most Basin in northern Bohemia supports previous results (Knor et al., 2012). Nevertheless, some further aspects should be discussed and broader comparisons should be made. Both horizons clearly differ one from another in respect of frequency and diversity of galls (Fig. 3). The gall frequency in LCH is 2.48 times higher than in DSH, which is the most significant difference among all kinds of observed plant–arthropod interactions. In terms of the gall diversity, there are two different methods

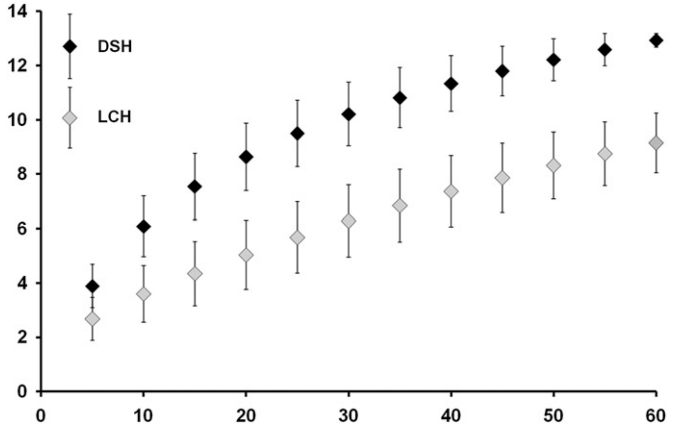



**Fig. 5.** Rarefaction curves — diversity of galling damage types rarefied to their own occurrence. Error bars indicate standard error of the mean.

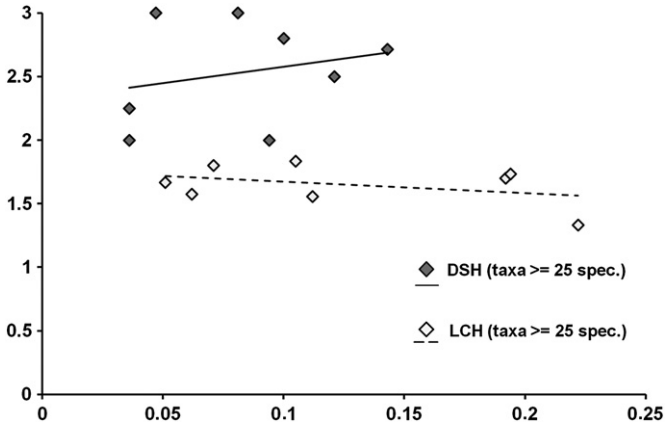



**Fig. 6.** Comparison of proportionality between the frequency of galls and the gall diversity rarefied to the three galling occurrences in case of both horizons. Vertical axis — gall diversity, horizontal axis — gall frequency. LCH — $R^2 = 0.228484$, $p = 0.279$; DSH — $R^2 = 0.063001$, $p = 0.549$.

of its settings, which should be mentioned. First, a comparison of the galling DT's diversity depends on the type of rarefaction procedure that was chosen. The diversity rarefied to the number of specimens (Fig. 4) is tightly connected with the frequency of damage occurrences, and therefore not suitable for certain types of analyses. On the other hand, rarefaction of the galling diversity to the number of their own occurrences (Fig. 5) reflects the original diversity of galling types for the complete dataset as well as for individual taxa, since it is not influenced by their frequency. These different approaches thus provide different outcomes. For assessing the proportionality between frequency and diversity in both horizons it is necessary to apply the second approach, since the influence of the damage frequency on the rarefied diversity must be eliminated. The observed correlation indicates the presence of a less diversified galling insect community in the LCH that caused more lesions than in the DSH (Fig. 6). Plant taxa in the LCH show a decrease in diversity towards the higher frequency of galling. The reason is probably the presence of dominant specialised galling guilds on the most affected taxa. Contrary, the DSH is characterised by a much higher diversity of these damages despite the lower galling frequency (Fig. 6). This is particularly apparent in the comparison of the diversity rarefied to the number of galling occurrences. The reason for this effect can be seen in the higher population density, together with lower taxonomic diversity of galling arthropods in the LCH. The palaeoenvironments seem to be predominantly determined by different climatic conditions, which were noticeably colder and drier in case of the LCH. Under those circumstances there was a lower diversity of galling insects in general, but according to the lower level of precipitation there was higher activity of a few galling taxa and thus a much higher frequency of galling damage.

### 5.2. Taxonomic determination

In the systematic part we have described the different types of fossil galls induced by various causers on angiosperm leaves and gymnosperm needles of ten species of host plants belonging to ten plant families from the lower Miocene of the Bílina Mine. Five fossil galls were probably induced by Cecidomyiidae (Diptera), six by Eriophyidae (Acari), and members of the Psyllidae (Hemiptera) and Cynipidae (Hymenoptera) each caused one gall type (Table 4).

Two genera of fossil plants, *Podocarpium* and *Decodon*, are new hosts of gall-induced organisms and nine species are new hosts of genera previously known as hosts of other species. All fourteen types of fossil galls found in the lower Miocene of Bílina Mine are new records for the Czech Republic.

Nevertheless, there will be some uncertainty in the true identification of fossil galls as in most cases we have only the two dimensional phenotypic expression whose lack of morphological characters precludes more specific identification of the causer (e.g., Scott et al., 1994; Labandeira and Phillips, 1996). On the other hand, a majority of gall-inducing arthropods display high level of affinity to particular host plant species and specific organ (e.g., leaves), for instance many gall midges are specific to the foliage of *Betula* L., 1753, *Quercus* L., 1753 and *Salix* L., 1753 (Skuhravá et al., 1984). Arthropod-induced galls are generally of bilateral or radial symmetry in opposite of galls induced by bacteria or fungi (Raman et al., 2005b). The observed morphological traits are mostly species-specific and they are often distinguishable as far as on sub specific level (Crespi et al., 1997; Inbar, 2006). We presume that fossil arthropod galls caused on host plants some 20 millions years ago were induced by the close relatives of recent gall-inducing species, most probably belonging to the same genus (e.g., Wappler et al., 2010). Our assumption is supported by the fact that the form, size and position of fossil galls on host plant organs, usually leaves, is very similar to those induced by recent species. Fossil galls are also associated with the same or with very closely related host plant genera as recent ones, so if we take into account their morphological similarities with recent galls, it is possible to suppose their close mutual relationship. Furthermore, based on external morphology and rich evolutionary history of certain gall-inducing species such as gall midges we could infer a rather slow rate of evolutionary changes during the Cenozoic (Nel and Prokop, 2006).

Skuhravá and Skuhravý (2010) attempted to elucidate the possible co-evolution of gall midges (Diptera: Cecidomyiidae) with several groups of plants in the geological history. Gall-inducing and plant-inhabiting gall midges of the subfamily Cecidomyiinae probably first developed during the Mesozoic (Roskam, 1985; Labandeira, 2005) when they started to interact with newly evolved groups of plants,

**Table 4**
Selected identifiable fossil galls associated with fossil host plants from the lower Miocene of Bílina mine, Most Basin (Czech Republic).

| Plant family | Host plant species | Taxonomical group of organisms inducing fossil galls | Recent gall-inducing species showing the closest resemblance |
|---|---|---|---|
| Cupressaceae | *Taxodium dubium* | Diptera: Cecidomyiidae | *Taxodiomyia* sp. |
| Lauraceae | *Daphnogene polymorpha* | Acari: Eriophyidae | *Eriophyes daphnogene* — extinct |
| Lythraceae | *Decodon gibbosus* | Diptera: Cecidomyiidae | *Horidiplosis ficifolii* |
| Fabaceae | *Podocarpium podocarpum* | Diptera: Cecidomyiidae | *Meunieriella aquilonia* |
| Betulaceae | *Alnus julianiformis* | Acari: Eriophyidae | *Eriophyes inangulis* |
| Fagaceae | *Quercus rhenana* | Hymenoptera: Cynipidae | *Cynips quercusfolii* |
| | *Trigobalanopsis rhamnoides* | Acari: Eriophyidae | *Eriophyes* sp. |
| Juglandaceae | *Carya* sp. | Hemiptera: Phylloxeridae | *Phylloxera caryaeglobuli* |
| Tiliaceae | *Tilia brabenecii* | Diptera: Cecidomyiidae | *Physemocecis hartigi* |
| Sapindaceae | *Acer angustilobium* | Acari: Eriophyidae | *Aceria pseudoplatani* |
| | | Acari: Eriophyidae | *Aceria macrochela* |
| Oleaceae | *Fraxinus bilinica* | Acari: Eriophyidae | *Aceria fraxinicola* |
| | | Acari: Eriophyidae | *Aculus epiphyllus* |
| | | Diptera: Cecidomyiidae | *Dasineura fraxinea* |

and inhabit suitable parts, organs and tissues inducing changes that initiated the formation of galls. The main development of gall-inducing and plant-inhabiting gall midges was during the Paleogene and Neogene, together and parallel to the development of flowering plants, as is supported by evidence of several fossil galls of gall midges (e.g., Wappler et al., 2010).

## 6. Conclusions

The rich North Bohemian taphocenosis of Bílina Mine and Břešťany Lagerstätten from lower Burdigalian/Eggenburgian offer the rare opportunity to study the exceptionally preserved galls on many fossil leaves of different plant taxa. Significant differences in diversity and frequency of the galls can be traced between older strata of Holešice Member (DSH) and the younger ones of Libkovice Member (LCH). The most probable explanation lies in the distinct environmental circumstances, namely in climatic conditions. Much drier, but colder climate with unevenly distributed rainfalls seems to have prevailed during the younger period, as can be judged from the nearly two and half fold increased level of gall frequency, but apparently lower diversity of all types of damage including galls. This finding proves the existence of abrupt climatic oscillation during the lower Miocene preceding the much later ones of Pliocene and Pleistocene times.

Many of the studied galls show a striking resemblance with the recent ones, especially concerning their external appearance and host plant specificity, allowing the closer taxonomic determination of their potential causer. Some of them are attributable to recent insects' or mites' families or even genus, providing their relatively long evolutionary stasis.

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## Článek III

**Knor, S.**, Kvaček, Z.,Wappler, T., Prokop, J., 2015. Diversity, taphonomy and palaeoecology of plant – arthropod interactions in the lower Miocene (Burdigalian) in the Most Basin in north-western Bohemia (Czech Republic) **Review of Palaeobotany and Palynology** accepted, in press. [IF 1.656]


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# Diversity, taphonomy and palaeoecology of plant-arthropod interactions in the lower Miocene (Burdigalian) in the Most Basin in north-western Bohemia (Czech Republic)

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## Abstract

An extensive collection of nearly 4200 fossil plants remains from lower Miocene deposits at Bílina and Břešťany were examined for signs of damage caused by arthropods. Determing the frequency and diversity of plant-arthropod interactions was the main objective, followed by a comparison of the level of damage to plant taxa for which there were at least 25 specimens. There were significant differences in the frequencies of the damage caused by the different functional feeding groups in the whole assemblage and individual taxa. Comparison of the diversity of the different types of damage by rarefying their five occurrences also confirmed the differences in the levels attained. The highest diversity was recorded for deciduous trees (*Alnus*, *Nyssa* and *Populus*). The organisms that caused some

of the highly specific types of damage, such as mining and oviposition, were taxonomically identified on the basis of their unique morphological traits. There was one remarkable non-herbivore plant-arthropod interaction represented by a solitary record of a caddisfly case built exclusively of *Taxodium* needles.

**Keywords**

damage type, functional feeding group, herbivory, Most Basin, Miocene, plant-arthropod interactions

## 1. Introduction

The interactions between herbivorous arthropods and their host plants make up a substantial part of the complex and intricate network in all terrestrial ecosystems. The features, intensity and diversity of these inter relationships are often influenced by current and past climatic and environmental conditions (Wilf and Labandeira, 1999; Wilf at al., 2001; Labandeira et al., 2002; Wappler, 2010; Wappler and Denk, 2011; Prokop et al., 2010; Labandeira and Currano, 2013). Specific aspects like the physiology of the plants, soil chemistry and nutrients are also probably important (Fernandes and Price, 1991; Cuevas-Reyes et al. 2003).

Well-preserved fossil plant assemblages are one of the best sources of current knowledge about the processes that have occurred throughout geological history (Bůžek et al., 1998; Kvaček, 1998). There is also a diverse range of different traces of feeding and non–feeding by arthropods present on the surface of fossil leaves. Most of them are unique in form allowing them to be classified into distinct so called functional feeding groups (FFGs), each containing a large number of so called damage types (DTs) (Cummins and Merritt, 1984; Labandeira et al., 2007). Comparison of the frequency and diversity of DTs occurring at different stratigraphic levels offers an excellent

opportunity to test the current hypothesis of the mutual relationships between the factors mentioned above (Knor et al. 2012; Wappler et al. 2012). The same is true for similar comparisons of particular species of plants in terms of different levels of specific DTs associated with distinct FFGs. The former is the main objective of the present study of the relatively rich fossil plant assemblages at Bílina and Břešťany situated in a brown coal basin in north-western Bohemia. We not only recorded the pattern of the different types of damage to dicotyledonous plants, but also other specific cases of non-herbivory events, like oviposition and a rare trichopteran case made of *Taxodium* needles.

## 2. Stratigraphy and palaeoenvironmental setting

The localities at Bílina Mine and Břešťany are the most spectacular in the the area of the large Most Basin situated in north-western Bohemia (Fig. 1). The basinal sedimentary fill, i.e. the so called Most Formation, is traditionally subdivided into four stratigraphic members (Pešek et al. 2014). The lowermost Duchcov ("Underlying") Member consists of redeposited volcanic clay and aluminium-rich claystone. The next above Holešice Member is a complicated sedimentary sequence, which includes the Main Coal Seam variously replaced by clastic sediments. It is overlain by the lacustrine Libkovice Member and the last, uppermost Lom Member (Domácí, 1977, Pešek et al., 2011, 2014). In the area of the Bílina Mine the upper part of the Holešice Member is developed in the delta facies and belongs to the most important fossiliferous layers. It can be further subdivided into the "Clay Superseam Horizon" with an "Upper Seam" and the younger "Delta-Sandy Horizon". Both the above mentioned stratigraphic sequences (as a part of the Bílina Mine) consist of several distinct layers reflecting different depositional environments (Bůžek et al., 1987; Kvaček et al. 2004) (Fig. 2). The three most important are those that originated during the period of weathering and sheet-wash, and the succession from peat swamp to alluvial plain and the deepening to form a lake basin ("Lake Clay Horizon") (Bůžek et al., 1992). Deposits in the two latter stages contain a wealth of fossil plant remains. The rocks

underlying the main coal seam are assigned to mammal zone MN3a, early Burdigalian (~early Eggenburgian) (Fejfar, 1989; Fejfar and Kvaček, 1993). These clay sediments with fossil animal remains are relatively poor in plant megafossils. Lowland swamp forest with evergreen oak *Quercus rhenana* (Kräusel et Weyland) Knobloch et Kvaček and *Glyptostrobus europaeus* (Brongniart) Unger prevailed during the early stages of the brown-coal swamp. Riparian elements (*Taxodium*, *Acer*, *Alnus* and *Toddalia*) or Lauraceae occur much more rarely. A more mesophytic forest with pines and evergreen Lauraceae covered sandy soils on crystalline rock at the periphery of the Ore Mts (Krušné hory in Czech). Later on mires developed and covered vast areas of the basin due to the constant high level of the underground water table. They were covered by dispersed stands of *Glyptostrobus* and other "coal-forming" trees with *Calamus*, patches of Zingiberaceae and aquatic plants. The forests in mineral swamps at the periphery were mainly deciduous, and more varied in composition, with *Salix*, *Nyssa*, *Alnus*, *Acer*, *Fraxinus* and *Taxodium* as dominant trees (Fejfar and Kvaček, 1993).

There are records of insect fossils, especially for Bílina, consisting of almost 350 specimens belonging to 11 orders (Prokop, 2003). Several species are well linked to other Neogene localities (e.g., Prokop and Nel, 2000; Fikáček et al., 2008; Wappler et al., 2013).

## 3. Taphonomy

Most of the leaves are well preserved as carbonized compressions lacking severe damage resulting from transport over great distances by wind or water, which indicate their autochthonous or parautochthonous origin. Leaves were deposited in thin layers apparently in offshore anoxic fine grain sediments. Some of them are so well preserved that it is possible to see fine details on their epidermis, which can be used for identifying them (Sakala, 2000; Teodoridis and Kvaček, 2006). In addition, arthropod mines, galls and other delicate structures are also well preserved. Many of the leaves, in addition to arthropod damage, also show signs of decomposition, which can be clearly distinguished by

the absence of a reaction rim, which is typical of herbivore damage (Labandeira et al., 2007). Other leaves show the presence of fungi, some of which were possibly parasitic, and others, decomposers of dead leaves. There are a few records of pieces of bark from taxonomically unidentified trees or shrubs with Pyrenomycetes, implying the secondary transport of partly rotten wood into a water environment. The whole assemblage thus seems to be a mixture of fallen leaves and living leaves detached by strong wind, both of which in certain cases bear signs of arthropod damage.

Besides the leaves, there are also fruit, cones and other reproductive plant organs, some of them of known taxa. There are rare records of whole branches together with leaves and reproductive structures suitable for complex plant reconstruction according to the so called "Whole-plant" concept (Kvaček, 2008).

## 4. Material and methods

The material studied is housed in the National Museum in Prague and the Bílina Mine enterprise collections including the private collection of Mr Zdeněk Dvořák. These collections consist of a total of 3509 fossil dicotyledonous leaves from 23 fossiliferous layers. Abbreviation prefixes of the collection numbers indicate either the National Museum in Prague (G-), Bílina Mine enterprise (DB-) or private collection of Mr Zdeněk Dvořák (ZDI-). All these leaves were examined for damage caused by arthropods and the type of damage was categorized based on its position, size and morphology following the method of Labandeira et al. (2007). The different types of damage (DTs) were then classified into one of eight functional feeding groups (FFGs): hole feeding (HF), margin feeding (MF), skeletonization (S), surface feeding (SF), galling (G), mining (M), piercing and sucking (PS) and oviposition (O) as described by Labandeira et al. (2002, 2007). In order to compare the incidence of the different FFGs at Bílina with those recorded at other localities (e.g. Svalbard), rarefaction procedures were applied, using the rarefaction method without repetition. This was done using the Vegan Package

implemented in the R statistics environment (R Development Core Team, 2009). The sample size was standardized by selecting a random subset of 50 leaves without replacement and the diversity of damage (all damage types, specialized damage types, galls and mines) for corresponding samples calculated. This process was repeated 5000 times and the results averaged to obtain a standardized diversity of damage. The same procedure was used to standardize the overall diversity of damage rarefied to the number of occurrences of all the taxa based on at least 25 leaves prior to comparing them. Further issues included setting the level of damage in an assemblage based on the whole dataset and all affected taxa in terms of particular FFGs, which corresponds to the proportional occurrence of damage and percentage of leaves damaged.

Special attention was given to specific types of damage that could be attributable to certain arthropods. In addition to the plant-arthropod herbivore associations represented by specific recognizable types of damage to the leaves of various dicotyledonous plants, a remarkable trichopteran fossil case built of *Taxodium* needles, which is a non-herbivore interaction between insect and gymnosperm plant, was also studied.

Each leaf with a specific type of damage or its impression (see Plates I, II) was photographed using a Canon D550 camera with a reversed MP-E 65 mm lens or an EF-S 60 mm lens. Original photographs were processed using the image-editing software Adobe Photoshop 8.0.

The sub-chapter *5.2. Review of leaf morphotypes* introduces plant taxa for which there are some damaged specimens together with their collection numbers. Four summary tables (Tab. 1–4) of all the taxa (including non-damaged ones) are also provided. The general plant systematics adopted was that of Taylor et al. (2009) and Reveal (2010, 2012).

## 5. Results

### *5.1. General quantitative evaluation*

The whole assemblage consists of almost 4300 specimens of dicotyledonous and monocotyledonous angiosperm leaves, gymnosperm branchlets, cones and bark fragments of unidentified trees or shrubs. Our quantitative analysis focused on 3509 dicotyledonous specimens, since the other groups of plants lack statistically significant levels of damage caused by arthropods. Galls on *Taxodium dubium* (Sternberg) Heer were the only exception (Knor et al., 2013).

In total 22.8 % of the leaves were damaged, which is 1015 separate records of damage, which can be categorized in terms of 60 distinct types. In terms of abundance hole-feeding is the most frequently recorded FFG, with the highest DT/leaf, followed by margin-feeding and galling, while oviposition together with piercing and sucking are the least abundant (see Tab. 5). Most of the damaged leaves have only one type of damage as is the case for FFGs. The number of leaves with more than one type of DT or FFG, respectively, declines exponentially with increase in the number of different DTs and FFGs (see Tab. 6)

Among the plant taxa with at least 25 specimens recorded in the census, *Populus zaddachii* Heer var. *brabenecii* Teodoridis has the highest level of damage with 0.816 DTs per leaf. The other taxa are substantially less affected, although more than half of them (21) surpass the average level of damage (Tab. 7, Figs 3, 4). The percentage occurrence of individual FFGs differs significantly for all the above-mentioned taxa, as can be seen in Fig. 3. Excluding the extremely rare FFG, piercing and sucking, which was not recorded for these taxa, only the leaves of *Quercus rhenana* **(**Kräusel et Weyland) Knobloch et Kvaček bear signs of the activity of all seven of the remaining FFGs. Leaves of further two taxa, *Acer tricuspidatum* Bronn and *Populus zaddachii* var. *brabenecii*, each bear signs of the activity of six distinct FFGs, whereas, by way of contrast those of *Comptonia difformis* (Sternberg) Berry and *Rosa europaea* (Ettingshausen) Kvaček et Hurnik are damaged only slightly and show signs of the activity of only one FFG. For these taxa, as is the case for the whole plant assemblage, hole- and margin-feeding are the most common and frequent FFGs, while oviposition is the rarest and only recorded for two taxa,

*Quercus rhenana* and *Salix haidingeri* Ettingshausen. For both these taxa, there is only one record of oviposition. Galling and mining were recorded for 26 and 14 host plant taxa, respectively (Fig. 3). Skeletonization is a relatively rare FFG in terms of the number of affected taxa, although in some cases, for instance *Laurophyllum pseudoprinceps* Weyland et Kilpper and *Liquidambar europaea* A. Braun, a substantial percentage (almost one third) of the damage is attributed to this FFG. Surface feeding is rarely recorded, both in terms of frequency and number of affected taxa (Fig. 3).

Comparison of diversity in terms of the categories of damage selected was the second most important aspect all of these 39 taxa (Tab. 7). This was solved in two sequential steps. The first was the rarefaction of types of damage into five occurrences. Diversity of damage caused by monophagous arthropods and characterized by a high degree of specificity, implies an equal diversity of host specific herbivores (Labandeira et al., 2002). Unfortunately, for only a few of the taxa studied were there a sufficient number (five) of records of damage caused by host specific herbivores for such an analysis. There is only output data for ten such taxa. Attacking two of the taxa, *Alnus gaudinii* (Heer) Knobloch et Kvaček and *Nyssa bilinica* (Unger) Kvaček (including *N. haidingeri* (Ettingshausen) Kvaček et Bůžek), there were five distinct specialist herbivores. For the other two taxa, *Populus zaddachii* and *Quercus rhenana,* more than four specialized DTs were recorded. The second step involved damage in general. The highest diversity in terms of total damage was recorded only for *Rubus merianii* (Heer) Kolakovskii, with five distinct types of damage although for the other ten taxa more than four distinct DTs were recorded. These outputs are very difficult to interpret, as more important factors should be considered. This will be considered in more detail in the Discussion.

*5.2. Review of leaf morphotypes*

**Conifers**

**Order Coniferales**

**Family Cupressaceae**

**Genus *Taxodium* L. C. M. Richard**

***Taxodium dubium* (Sternberg) Heer**

Sterile twigs have flattened, distichously arranged needles (10–14 mm long, ca 1.5 mm wide), which alternate at unequal distances, have acute apices and their bases are often very shortly petiolate and obtuse; the venation has a charistically strong and prominent midrib (Teodoridis and Sakala, 2008). This extinct species differs only slightly in most of its morphological and ecological aspects from the living species of this genus, which occur in lowland swamp forests in the southeastern United States (*Taxodium distichum* (L.) Richard) and Mexico (*T. mucronatum* Tenore) (Kvaček, 1976).

There are 133 branchlets of this taxon, some of which have globular corpuscles that are thought to be cecidomyiid galls (Knor et al., 2013) (see also Plate I. 1, 2). There is also a unique finding of another type of non–herbivore insect–plant interaction, which was not classified as damage. In specimen ZD0151 (Plate I. 3) there are several fragments of elongated structures, 25–35 mm long and 8.6 mm wide, composed of *Taxodium* needles. Eight to ten of these needles placed side by side are arranged in a succession of regularly repeating transverse rows, each overlapping the distal end of the previous one. This type of arrangement is very similar to that of a caddishfly case (Trichoptera), although no fossil remains of this insect were found in association with this structure.

**Angiosperms**

**Order Laurales**

**Family Lauraceae**

**Lauraceae gen. et. sp. indet.**

Collection number s of the fossil material: DB57-6208, DB2-6015, DB3-263a, DB3-263b, DB32-6017, DB32-6018, DB36-212, DB36-231, DB36-328, DB36-6019, DB39-016, G-3903, G-3904, G-3905, G-3907, G-3908, G-3920, G-3921, G-3923, G-3926, G-5429, G-9030, G-9038, G-9040, G-9045, G-9047, G-9048, G-9053, G-9064, G-9077, G-9095, G-9157, G-9159, G-9169, G-9171, G-9179, G-9191, G-9198, G-9201, G-9204, G-9207

Leaves of most Lauraceae are very difficult to classify without knowledge of other anatomical details (cuticle, reproductive organs), so their relationship with recent taxa remain uncertain. They are pinnately veined and of uniform shape with a noticeably irregular course of secondary veins. This family includes typically thermophilous plants and the presence of their leaves indicate global and local warming events. Based on their occurrence and the accompanying plant assemblage, members of Lauraceae grew on drier and more acid depleted substrates (Kvaček, 1971).

The taxon Lauraceae gen. et sp. indet. includes a set of 253 moderately damaged leaves, the second most abundant belonging to the order Laurales. Margin- and hole-feeding are the most frequently recorded FFGs, followed by galling.

**Genus *Daphnogene* Unger**

***Daphnogene polymorpha* (A. Braun) Ettingshausen**

Collection numbers of the fossil material: DB32-294, DB32-278, DB32-283, DB32-284, DB32-286, DB32-320, DB32-5656, DB32-5657, DB32-5658, DB32-5659, DB32-5661, DB32-5662, DB32-5663, DB41-5651, DB41-5652, DB41-5653, DB41-5654, DB41-5655, DB41-5660, G-1819, G-1820, G-1822, G-1823, G-1836, G-2464, G-2502, G-2509, G-2511, G-5451, G-5453, G-573, G-684, G-690, G-691, G-693, G-701, G-703, G-711, G-712, G-714, G-717, G-718, G-818, G-823, G-826, G-878, G-882, G-9150, G-9152, DB11-105

***Daphnogene* sp.**

Collection numbers of the fossil material: DB36-5726, B73-102

Leaves are elliptical to ovate, tri-veined, 50–60 (70) mm long and 20–30 mm broad, with a cuneate base, attenuate to the acute apex and with an entire margin (Teodoridis, 2001). This evergreen tree or shrub was a characteristic component of subtropical forests growing on elevated parts of the basin. The morphology of the fruits indicates a close relationship with *Cinnamomum camphora* (L.) J. Presl that currently occurs in subtropical and tropical Asia (Kvaček and Walther, 1974).

*Daphnogene polymorpha* and *Daphnogene* sp. make up a substantial part of the specimens of fossil Laurales. Damaged leaves are mostly affected by galls, in some cases attributed to identifiable causers (Knor et al., 2013). Hole-feeding is the second most frequent FFG, followed by margin-feeding.

**Genus *Laurophyllum* Göppert**

***Laurophyllum pseudoprinceps* Weyland et Kilpper**

Collection numbers of the fossil material: DB2-107a, DB32-6098, DB61-6096, DB61-097, G-3901, G-3959, G-453, G-862, G-9166, G-9308

***Laurophyllum saxonicum* Litke**

Collection numbers of the fossil material: G-3855, G-3857, G-3862, G-5409, G-7607, G-609, G-9270, G-9273, G-9274, G-9277, G-9280

***Laurophyllum* sp.**

Collection numbers of the fossil material: DB41-288B, G-3563, G-3568, G-3874, G-3929, G-3942, G-3943, G-3953, G-3956, G-3958, G-3964, G-3966, G-3985, G-3988, G-3993, G-3994, G-3997, G-7611, G-9305

*Laurophyllum saxonicum* (syn. *L. nemejcii*) is characterized by smaller, usually only 40–100 mm long leaves with slightly highlighted veins on the lower surface (Kvaček, 1971). It occurs in the Břešťany clays and is represented by relatively large, up to 200 mm long, leaves. The members of the genus *Persea* Miller are considered to be the nearest living relatives. *Laurophyllum pseudoprinceps* appears in the sandy-clayey sediments and clays mainly in lacustrine facies.

All three taxa are affected mostly by margin-feeding and galling.

**Order Magnoliales**

**Family Magnoliaceae**

**Genus *Magnolia* L.**

**cf. *Magnolia kristinae* Knobloch et Kvaček**

Collection numbers of the fossil material: DB36-6217, DB36-6231, DB41-330, DB41-210, DB41-6215, DB41-6216

Leaves are oval, 45–55 mm wide and 80–100 mm long, entire-margined and chartaceous. Like some other members of this the genus, *Magnolia kristinae* was probably a deciduous tree more common in mastixioid floras (Wackersdorf, Hrádek part of the Zittau Basin - Knobloch et Kvaček 1976). Species of *Magnolia* currently usually occur in either zonal or wetland habitats (Kovar-Eder et al., 2008). The affinity of this morphotype has been lately questioned and transferred to legumes (Holý et al. 2012).

This species is moderately damaged, mostly by margin-feeding.

**Order Piperales**

**Family Aristolochiaceae**

**Genus *Aristolochia* L.**

***Aristolochia* sp.**

Collection number of the fossil material: DB57-308

Leaf is broad, 110 mm wide and 85 mm long, with a medium acute apex and wide obtuse base. Living members of this genus grow usually in lowlands at the margins of tropical or subtropical forests (Huber, 1993).

The single specimen has two feeding holes.

**Order Proteales**

**Family Platanaceae**

**Genus *Platanus* L.**

***Platanus neptuni* (Ettingshausen) Bůžek, Holý et Kvaček**

Collection numbers of the fossil material: DB32-287, DB32-6464, DB32-6466, DB32-6467, DB32-6468, DB41-6465

Leaves range from simple to trifoliolate and sometimes quinquefoliolate with unlobed elliptical to obovate laminae, about 80 mm long, with uniform venation, marginal serration and epidermal structures. Twigs with leaves confirm that the leaves were deciduous (Kvaček and Manchester, 2004). *Platanus neptuni* was a conspicuous warm–temperate to subtropical element in European floras from late Eocene to late Miocene.

This species is represented by 16 leaves, which show relatively high levels of damage mainly due to hole-, margin-feeding and skeletonizing arthropods.

**Order Ranunculales**

**Family Berberidaceae**

**Genus *Berberis* L.**

***Berberis berberidifolia* (Heer) Palamarev et Petkova**

Collection numbers of the fossil material: DB57-325, DB24-5412, DB32-5408, DB33-5411, DB41-324, DB41-5407, DB57-5409, DB57-5410, G-7620

Leaves simple, obovate, up to 80 mm long, with a long decurrent base, margin entire to widely spinely serrate, texture firm. Based on the shape of the leaves and arrangement of the veins all the specimens belong to an extinct species of the genus *Berberis*. Members of this genus occur in open forests throughout the northern hemisphere. *Berberis berberidifolia* was certainly xeric and thermophilic, like most the extant species (Palamarev and Petkova, 1987).

The 56 specimens of this taxon in the collection indicate it was fairly abundant. Its leaves were only moderately damaged by arthropods, with margin-feeding the most frequent FFG.

**Order Saxifragales**

**Family Cercidiphyllaceae**

**Genus *Cercidiphyllum* Siebold et Zuccarini**

***Cercidiphyllum crenatum* (Unger) R. W. Brown**

Collection numbers of the fossil material: DB30-347, DB30-346, DB1-127, DB1-258a, ZDI0012, DB5-348, DB5-5575, DB48-157d

Leaves are elliptical to broadly ovate to rounded, palmately 5-veined with entire or finely crenulate margins (Jähnichen et al., 1980), 50–100 mm in diameter, chartaceous. This small deciduous tree probably had slightly different environmental requirements than the two extant species. Based on its common presence in coal facies, it can be inferred that this species inhabited swamp and lowland habitats around marshes. Nearest relatives survive as relicts in Japan and China, where they grow in damp river valleys.

This taxon was moderately affected by ten DTs belonging to three FFGs. Galling was the most frequent and most diverse.

**Family Hamamelidaceae**

**Genus *Liquidambar* L.**

***Liquidambar europaea* A. Braun**

Collection numbers of the fossil material: DB5-133, DB36-210, DB5-136, DB5-180, DB5-184, DB5-351A, DB24-187, DB24-188, ZDI043, DB27-6168, DB32-6169, DB36-206E, DB36-6170, DB39-6167

Leaves are palmately tri- to five-lobed, lobes oblong to triangular, 40–150 mm wide and up to 100 mm long, base shallowly cordate to cordate, apices acute. Margins are regularly crenulate. *Liquidambar*

*europaea* was a riparian deciduous tree. Its nearest living relatives are also trees growing in moist or wet soils near rivers and marshes on the East coast of USA and Mexico (e.g., *Liquidambar styraciflua* L.). Another closely related species *Liquidambar orientalis* L. survives as a relict in damp valleys in the Near East and on adjacent islands (Rhodes) (Gregor, 1993).

This species is relatively abundant and moderately damaged. Skeletonizations, hole-feeding and mining are the most common causes of damage. Two specimens (DB5-180, DB5-184), both bear a special type of blotch mine, characterized by its circular shape and a distinct dark outline with pellets dispersed inside.

**Genus *Parrotia* C. A. Meyer**

***Parrotia pristina* (Ettingshausen) Stur**

Collection numbers of the fossil material: DB1-120, DB1-126, DB5-141, DB5-6397, DB17-6398, DB36-165a, DB36-165b, DB36-205, DB36-222, DB36-6396, DB36-6400, B36-6401, DB36-6404, DB36-6405, DB61-6393, DB61-6394, DB61-6395, DB61-6399, DB61-6402, DB61-6403

Leaves are broadly oval to obovate with obtuse apex, coarsely undulate margins, up to 50 mm long. *Parrotia pristina* was a deciduous woody species of wetter slopes. This species was widespread throughout Eurasia in the early Miocene. It has two close relatives that are currently still extant in two small areas in northern Iran (*Parrotia persica* C.A. Meyer) and eastern China (*Parrotia subaequalis* (H.T. Chang) R.M. Hao et H.T. Wei) and are large deciduous shrubs or small trees (Knobloch and Kvaček, 1976).

This species is represented by 66 specimens with a high level of damage. The most frequent FFG is hole-feeding.

**Order Vitales**

**Family Vitaceae**

**Genus *Ampelopsis* A. Michaux**

**cf. *Ampelopsis* sp.**

Collection numbers of the fossil material: DB5-5378, DB5-5379

Leaves are coarsely toothed, palmately lobed with broadly triangular lobes, ca. 60 mm wide and 60–120 mm long; texture chartaceous. Due to the few fossils the relationships of this taxon remains unclear. Leaf morphology is similar to that of the genus *Ampelopsis*.

Seven specimens are available of which two bear hole-feeding damage.

**Genus *Vitis* Adanson**

***Vitis stricta* (Göppert) Knobloch**

Collection number s of the fossil material: DB36-183a, DB36-219, DB36-220, DB36-339, DB36-6960, DB36-6961, G-5494

Leaves are asymmetrical, palmately three-lobed, with acute apex and broadly or deeply cordate base, up to 80 mm long. Their margins are irregularly dentate. This species of vine occurred at the edges of coastal forests like its recent relatives, which occur in mild subtropical to warm temperate zone forests in the northern hemisphere.

*Vitis stricta* shows a high level of hole and margin damage caused by arthropods.

**Order Myrtales**

**Family Lythraceae**

**Genus *Decodon* Gmelin**

***Decodon gibbosus* (E. M. Reid) E. M. Reid (="*Ficus" multinervis* Heer)**

Collection numbers of the fossil material: DB30-305, DB2-111b, ZDI0002, DB21-5817, DB1-114, DB2-109b, ZDI039, DB36-209, DB36-5799, ZDI0034, DB47-5797, DB47-, 798, DB47-5800, DB72-90, G-4500, ZDI044

The leaves have entire-margins and are linear to broadly lanceolate, 100–250 mm long and 15–55 mm broad, cuneate to long cuneate with long petioles (Teodoridis, 2001). This plant was probably a low growing shrub, which grew in shallow water in *Taxodium* swamp forests, based on the habitus of its nearest living relative, *Decodon verticillatus* (L.) Elliot, in eastern North America (Kvaček and Sakala, 1999).

About 40% of the leaves of this fairly abundant species are damaged by five distinct FFGs. Margin-feeding is the most frequently recorded damage, followed by hole-feeding. Of the four records of galling one is attributed to a gall midge (Knor et al., 2013).

**Order Fabales**

**Family Fabaceae**

**Leguminosae gen. et sp. indet.**

Collection numbers of the fossil material: DB1-128, DB2-6114, DB4-174, DB4-6118, DB24-190, DB24-6116, DB32-6112, DB39-6113, DB39-6117, DB48-6115

This diverse group of taxonomically closely related but undefined specimens, which belong to the Fabaceae, bear a rather lower degree of damage. Hole-feeding is the most frequent and diverse FFG. There is also one record of rare surface feeding.

**Genus *Leguminosites* Bowerbank *sensu* Schimper**

***Leguminosites* sp. div.**

Collection number of the fossil material: G-7627

Leaflets are usually of regular oval shape with a rounded apex and entire margin, 10–60 mm long (Kvaček et al., 2004). There is nothing certain about the palaeoecology of these species. They are thought to be xerophilic, because extant species occur mainly in the African savannah but in North America and East Asia they regularly occur in wet climate forests. Their accurate identification and

taxonomic relationships with the extant species are usually impossible to establish because of the uniformity of their leaves. Legumes generally have compound leaves, which are rarely preserved intact.

A single specimen bears piercing and sucking damage, which is the rarest FFG recorded in this assemblage.

**Genus *Podocarpium* A. Braun ex Stizenberger**

***Podocarpium podocarpum* (A. Braun) Herendeen**

Collection numbers of the fossil material: DB36-228c, DB36-5949, DB36-5950, DB39-5906, DB41-293, DB57-327, DB57-5948, DB57-5951

Leaflets are oval, 15–25 mm long and 8–10 mm broad with a narrow and rounded apex, an entire margin, a strong, straight midrib and one or more prominent camptomodromous basal veins (Teodoridis, 2001). This species is distantly related to some members of the Amherstieae and Detarieae in tropical Africa (Herendeen, 1992). It is probably a thermophilous and xerophilous shrub or tree, inhabiting elevated sites in the basin (Bůžek et. al., 1996). It is apparently a Paleogene-Neogene Eurasian element that has not yet been recorded in North America (Herendeen, 1992).

*Podocarpium podocarpum* is a fairly abundant taxon with a relatively low level of damage. Damage due to margin-feeding is the most frequent, followed by hole-feeding and skeletonization.

**Genus *Wistaria* Nuttall**

***Wistaria* aff. *fallax* (Nathorst) Tanai et Onoe**

Collection numbers of the fossil material: DB57-6971, ZDI042

Leaflets are broadly ovate, approximately 20 mm wide and 40 mm long, with wide obtuse apex, broadly cordate base and entire margin. Venation is brochidodromous with a straight midrib (Teodoridis, 2001). *Wistaria* aff. *fallax* occurred probably as a liana in offshore vegetation. FFGs are represented by hole-feeding with two distinct damage types.

**Order Fagales**

**Family Betulaceae**

**Genus *Alnus* Miller**

***Alnus gaudinii* (Heer) Knobloch et Kvaček**

Collection numbers of the fossil material: DB30-382, DB21-384, DB32-5192, DB21-235, DB21-236, DB21-241, DB21-247A, DB21-5155, DB24-195, DB24-5154, DB32-5143, DB32-5144, DB32-, 145, DB32-5153, DB36-183B, DB36-221, DB36-5147, DB36-5149, DB36-5150, DB36-5151, ZDI0006, DB39-5146, DB41-5148, DB41-5152, DB47-385, G-4507

***Alnus julianiformis* (Sternberg) Kvaček et Holý**

Collection numbers of the fossil material: DB3-254b, DB36-162, ZDI0028, ZDI037, ZDI0007, DB3-253, DB3-254a, DB3-255, ZDI0019, DB4-260, DB5-177B, DB5-5306, DB21-237, DB21-239, DB24-197, DB24-5294, DB24-5304, ZDI0025, DB32-5297, DB32-, 299, DB32-5301, DB32-5302, DB32-5305, DB32-5307, DB32-, 308, DB32-5313, DB32-5315, DB33-265h, DB33-265i, DB35-276, DB36-206a, DB36-206b, DB36-207a, DB36-207b, DB36-213a, DB36-216, DB36-217a, DB36-228b, DB36-5293, DB36-5300, DB36-5309, DB36-5310, DB39-296a, DB39-296b, DB41-291, DB41-5298, DB47-5295, DB61-5296, DB61-5303, DB61-5311, DB61-5312, DB61-5314, DB76-352, G-1672, G-1680, G-1698, G-1712, G-1722, G-1724, G-1730, G-1740, G-1764, G-1772, G-778, G-1779, G-1785, G-2133, G-2141, G-2143, G-3199, G-3213, G-3215, G-3218, G-3220, G-3221, G-3258, G-3292, G-3309, G-, 378, G-3379, G-3381, G-3383, G-3385, G-3507, G-3524, G-3546, G-3817, G-5356, G-5372, G-9214, G-9217

***Alnus menzelii* Raniecka-Bobrowska**

Collection numbers of the fossil material: DB61-277, DB21-243, DB21-5340

***Alnus* sp.**

Collection number of the fossil material: G-3299

**cf. *Alnus* sp.**

Collection numbers of the fossil material: DB36-230c, DB2-107b, DB5-138c, DB33-269, DB36-5353, DB36-5354, ZDI066b, ZDI066c

Leaves of *Alnus gaudinii* are elliptical to lanceolate, 15–30 mm wide and 50–80 mm long, with a cuneate base and an acute apex (Knobloch and Kvaček, 1976); texture chartaceous. This tree is considered to be a thermophilous and less hydrophilous species. Its nearest living relative is Himalayan alder (*Alnus nitida* (Spach) Endlicher). *Alnus julianiformis* has elliptical leaves, 45–55 mm long and 28–39 mm broad, with a short acute apex and cuneate base. Leaves are entire-margined basally and become simple-serrate with acute teeth distally. This species is one of the most common deciduous trees in our collection. In fact, it is the most abundant taxon in floodplain and swamp forest ecosystems. It shows a very close affinity to extant species of *Alnus* that occur in central China, e.g., *A. trabeculosa* Handel-Mazzetti (Kvaček and Holý, 1974). Large numbers of leaves of this tree are recorded in all horizons. Leaves of the last species, *Alnus menzelii*, are quite large, 8–12 cm long, broadly ovate and often cordate at the base (Kvaček and Hurník, 2000). This was a marsh dwelling deciduous tree whose leaves are often found in coal forming clays or porcelanite, especially at the southeastern edge of the basin.

All three species of alder show moderate levels of damage, with margin-feeding the most common FFG, followed by hole-feeding and galling. Some of the galls found on leaves of *Alnus julianiformis* are attributable to particular arthropods (Knor et al., 2013).

**Genus *Betula* L.**

***Betula* sp.**

Collection numbers of the fossil material: DB5-381, DB1-122a, DB1-5454, ZDI0015, DB24-5460, DB36-154, DB36-229a, DB36-386, DB36-5455, DB36-5456, DB36-5457, DB36-5458, DB36-5459, G-9324

Leaves are elliptical to ovate with broadly cuneate base and acute apex, 30 to 80 mm long and chartaceous. Entire margin at the base becomes irregularly double–serrated distally. Birch was a rare element in floodplain forests.

*Betula* sp. belongs to taxa showing relatively high degrees of damage, mainly due to hole- and margin-feeders. Galling and skeletonization are rarely recorded.

**Genus *Carpinus* L.**

***Carpinus grandis* Unger**

Collection numbers of the fossil material: DB1-124, DB41-5482, DB61-275, DB61-5481, DB61-5483

***Carpinus* sp.**

Collection numbers of the fossil material: DB5-138b, DB36-5494, DB36-5495

Leaves are oval to ovate, usually less than 120 mm long, chartaceous, with cuneate to slightly cordate base, acute apex and margin usually double serrate. Hornbeam is a member of the lower storey of deciduous temperate to subtropical forests.

Both taxa show moderate levels of damage, mainly due margin-feeders.

**Family Fagaceae**

**Genus *Quercus* L.**

***Quercus rhenana* (Kräusel et Weyland) Knobloch et Kvaček**

Collection numbers of the fossil material: DB2-152, DB5-185, ZDI046, DB24-153, DB24-173, DB24-178, DB24-193, DB73-6549, G-3969, G-3970, G-3972, G-5398, G-5399, G-7622, G-7624, G-7647, G-9127, G-9134, G-9135, G-9137

This extinct oak was a thermophilous and evergreen tree with long lanceolate to oblanceolate, entire-margined leaves, up to 400 mm long, growing in drier places in the brown-coal basin. The leaves of this

species are typical with a very stout midrib and petiole, and obviously coriaceous texture. *Q. virginiana* P. Miller occurring in North America is its closest living relative (Knobloch and Kvaček, 1976).

This fairly abundant species shows relatively high levels of damage. Some spectacular types of damage, such as certain types of galls and margin-feeding are recorded. Nevertheless, hole-feeding is the most frequent FFG, as is the case for most of the taxa studied.

**Genus *Trigonobalanopsis* Kvaček et Walther**

***Trigonobalanopsis rhamnoides* (Rossmässler) Kvaček et Walther**

Collection numbers of the fossil material: DB24-6791, G-9329

Leaves are elliptical to obovate in form, 30–40 mm wide and up to 120 mm long, with an acute apex, cuneate base and entire margin. Venation is regularly brochidodromous with a strong midrib. The genus *Trigonobalanopsis*, an extinct evergreen member of the family Fagaceae, was especially abundant during the warmer periods of the Neogene. This tree grew in acid soils on dry slopes. It is considered to be a European endemic, based on its occurrence. Similarly, a distantly related extant tree *Formanodendron doichangense* (A. Camus) Nixon et Crepet grows in mountain forests in Laos and Southern China (Nixon and Crepet, 1989).

Only three specimens were studied, one of which bears damage due to both galling and a margin feeder.

**Family Juglandaceae**

**Juglandaceae gen. et sp. indet.**

Collection numbers of the fossil material: DB61-5988, DB61-5989

This group is represented by only three leaflets of which two are damaged by two occurrences of hole-feeding and one of skeletonization.

**Genus *Carya* Nuttall**

***Carya serrifolia* (Göppert) Kräusel**

Collection numbers of the fossil material: ZDI0020, DB32-285, ZDI061, DB36-203, DB36-204, DB36-208, DB36-226a, ZDI065, DB39-5507, DB41-292, DB41-5508, ZDI063, ZDI0011

***Carya* sp.**

Collection numbers of the fossil material: DB39-298, ZDI0021, ZDI0018, DB57-379, DB74-151, DB2-262, DB32-282, DB32-5520, DB32-5526, DB32-5527, DB32-5528, DB32-5530, DB32-5551, DB36-211, DB36-223, DB36-225c, DB36-5522, DB36-5523, DB36-5525, DB36-5529, ZDI0028, DB41-288a, DB41-161, DB41-5521, DB57-5524, DB74-5547

Leaflets are usually oblong, elliptical to ovate, 45–100 mm long and 20–40 mm broad, with a cuneate base, an acute apex and a finely serrated margin (Teodoridis, 2001). Today, the genus *Carya* occurs in North America and East Asia, and exhibits a typical disjunct distribution. *Carya serrifolia* is a member of the floodplain forest plant assemblage occurring in the eastern part of North America (Bůžek, 1971). The nearest living relative of this species is *Carya poilanei* (Chevalier) Leroy that occurs in East Asia and has fruit of similar morphology (Czaja, 2003).

Both taxa are represented by 90 frequently damaged leaves, with hole-feeding and margin-feeding FFGs the most abundant, followed by galling. There are also two occurrences of mining.

**Genus *Engelhardia* Leschenault ex Blume**

***Engelhardia orsbergensis* (P. Wessel et C. O. Weber) Jähnichen, Mai et Walther**

Collection numbers of the fossil material: DB36-234, DB36-5777

Oblong leaflets with asymmetric sessile bases, up to 40 mm long have widely serrated margins, which form paripinnate leaves (Kvaček, 1972). *Engelhardia orsbergensis* was a thermophilic semi-deciduous tree that grew in damp slopes, and was widespread throughout Europe. Recent relatives are found today

in the subtropics of East Asia (*Engelhardia roxburghiana* Wall) and Mexico (*Engelhardia* (*Oreomunnea*) *mexicana* Standley).

*Engelhardia orsbergensis* suffered relatively little damage, inflicted by only two FFGs, namely hole- and margin-feeders.

**Genus *Juglans* L.**

***Juglans acuminata* A. Braun**

Collection numbers of the fossil material: DB30-323, DB1-113, DB1-117, DB27-5972, DB61-274, DB72-87

Leaflets are oblong to elliptical, 20–60 mm wide and 60–200 mm long, chartaceous, with slightly asymmetrical base, acute apex and entire margin. Venation is brochidodromous with a strong midrib. *Juglans acuminata* grew in a deltaic environment (Bůžek, 1971).

This species shows moderate levels of damage, caused equally by four FFGs, namely hole-feeding, margin-feeding, galling and skeletonization.

**Family Myriaceae**

**Genus *Comptonia* l'Héritier ex W. Aiton**

***Comptonia difformis* (Sternberg) Berry**

Collection numbers of the fossil material: DB1-5598, DB2-5595, DB2-5596, DB2-5599, DB39-5594, DB41-5597, G-2604, G-2610

Leaves are pinnately lobed, oblong to lanceolate, usually 120 mm, but also up to 200 mm long, with cuneate base and acute apex (Teodoridis, 2001). This deciduous shrub was characteristic of sandy soils and often accompanied *Pinus* spp., which has similar substrate requirements. The only current representative (*Comptonia aspleniifolia* Aiton) grows in forests in the Atlantic part of North America (Kotlaba, 1961; Bůžek, 1971).

This relatively abundant species suffered low levels of damage, with only eight occurrences of a single FFG recorded.

**Genus *Myrica* L.**

***Myrica banksiaefolia* Unger**

Collection numbers of the fossil material: G-8057, G-8058

***Myrica intergerrima* Kräusel et Weyland**

Collection numbers of the fossil material: DB32-6235, DB41-6236

***Myrica lignitum* (Unger) Saporta**

Collection numbers of the fossil material: DB2-259, DB24-6268, DB32-6267, DB41-6240, DB47-150, G-534, G-7625, G-8027, G-8044, G-8054, DB11-100, DB11-103, DB11-334, DB11-6241, DB11-6242, DB11-91, DB11-99

***Myrica* sp.**

Collection numbers of the fossil material: G-8006, G-8009a, G-8009b, G-8012, G-8014, G-8017, G-8018, G-8039, G-8043

*Myrica integerrima* has oblong to elliptical leaves, 100–150 mm long, with a narrow cuneate base, acute apex and entire margins. Leaves of *Myrica lignitum* are relatively more slender with often coarsely serrate margins (Knobloch and Kvaček, 1976). All *Myrica* species had a coriaceous leaf texture and were common components of swamp forming vegetation. *Myrica lignitum* grew also on acid soils on the surrounding slopes.

The genus *Myrica* is represented by more than 100 specimens, showing moderate levels of damage. Most common FFGs are hole- and margin-feeding, followed by galling.

**Order Malpighiales**

**Family Salicaceae**

**Genus *Populus* L.**

***Populus populina* (Brongniart) Knobloch**

Collection numbers of the fossil material: DB4-261, DB5-6507, DB32-367, DB32-6504, DB32-6505, DB32-6506, DB36-232, DB61-6503, DB61-6508

***Populus zaddachii* Heer var. *brabenecii* Teodoridis**

Collection numbers of the fossil material: DB23-390, ZDI0001, DB57-299, DB63-391, DB14-6483, DB24-388, DB29-6484, DB33-6482, DB36-215, DB36-225a, DB36-333, DB36-6485, DB47-155, ZDI036, ZDI049, ZDI051, ZDI055, ZDI056, DB48-389, ZDI0017, DB74-149, ZDI064

Leaves of *Populus populina* are rounded with broadly cuneate base and acute apex, typically 80 (up to 100 mm) wide and 50 mm long. Margin is regularly coarsely dentate (Bůžek, 1971; Knobloch and Kvaček, 1976). *Populus zaddachii* had leaves of ovate shape with a narrowly round to broad cuneate base and acute apex, 40–200 mm long, quite variable in shape. Margins are irregularly simply serrate to crenulate (Teodoridis, 2001). Both species are deciduous with chartaceous foliage. They were inhabitants of floodplain forest.

The leaves of *Populus zaddachii* were the most frequently damaged and by the highest diversity of FFGs. Nevertheless, hole-feeding was the major cause of the damage in both species.

**Genus *Salix* L.**

***Salix haidingeri* Ettingshausen**

Collection numbers of the fossil material: DB5-176, DB21-250, DB47-311, DB36-165D, DB36-230B, DB36-6641, DB36-6646, DB47-167, DB47-170, DB47-6642, DB47-6643, DB47-6644, DB47-6645, ZDI052, DB52-6640

***Salix* sp.**

Collection numbers of the fossil material: D36-264, DB18-6662, DB36-213B, DB47-166

***Salix varians* Göppert**

Collection number of the fossil material: DB24-6673

All willows have lanceolate to slightly ovate leaves with a cuneate to rounded base, acute apex and crenulate or serrate margins (Bůžek, 1971; Mai and Walther, 1978). Leaves of *Salix haidingeri* are quite narrow, with parallel margins and are only up to 10 mm wide and up to 200 mm long, whereas those of *S. varians* are broader, 30–40 mm wide and up to 90 mm long, distinctly glandular crenulate on margin (Kvaček et al. 2004). Both were characteristic deciduous components of the vegetation at the edge of coal forming swamps and bogs.

*Salix haidingeri* suffered the highest level of damage, by six FFG including the scarce damselfly oviposition on specimen DB21-250 (Plate I. 15, 16).

**Order Rosales**

**Family Celtidaceae**

**Genus *Celtis* L.**

***Celtis japeti* Unger**

Collection number of the fossil material: DB1-5564

Leaves are ovate to lanceolate, 15–50 mm wide and 40–120mm long, with asymmetrical base and entire to slightly serrate margin (Němejc et al., 2003). Today, hackberry grows as a mesophilic, thermophilic and deciduous tree in the northern hemisphere temperate zone and tropics.

Only three leaves of this species were found, one of them bearing two FFGs, hole- and margin-feeding.

**Family Rhamnaceae**

**Genus *Berchemia* Necker ex A. P. de Candolle**

***Berchemia multinervis* (A. Braun) Heer**

Collection numbers of the fossil material: DB1-112, DB1-123, DB1-5438, DB5-135, ZDI0013, ZDI0031

Leaves are elliptical, entire-margined and usually shorter than 80 mm, with dense eucamptodromous secondary venation. This creeper grew in coastal marshes and swamp forests based on its occurrence in the sand and coal facies. Current representatives with similar deciduous leaves grow in the wetland of floodplain forests in the southeast United States and East Asia. The closest species, *Berchemia scandens* (Hill) K. Koch, occurs in the *Taxodium* swamp forest in Florida (Bůžek, 1971; Kvaček et al., 2004).

This species suffered a moderate degree of damage, with three occurring FFGs. The most abundant is margin-feeding.

**Genus *Paliurus* P. Miller**

***Paliurus tiliaefolius* (Unger) Bůžek**

Collection numbers of the fossil material: DB36-229b, DB1-115a, DB1-301, DB36-224, ZDI0035, DB47-302, DB61-6368

Leaves are typically up to 80 mm in size, broadly cordate, margin finely serrated, triveined. *Paliurus tiliaefolius* was a deciduous spiny shrub, like its living relatives, bearing ovate triveined leaves with a round base and an acute apex (Teodoridis, 2001).

This taxon suffered moderate damage due to two FFGs, namely margin-feeding and more frequent hole-feeding.

**Family Rosaceae**

**Genus *Rosa* L.**

***Rosa europaea* (Ettingshausen) Kvaček et Hurnik**

Collection numbers of the fossil material: DB5-189, DB36-6576

Leaflets of this rose are relatively small, up to 40 mm long, obovate to ovate, usually sessile, with dense venation and finely serrate margin. This rose was probably a part of the shrubby undergrowth in lowland forests. It occurs almost exclusively in the sandy-clayey layers of deltas at both Bílina and Žatec (Bůžek, 1971; Kvaček and Hurník 2000).

This relatively abundant taxon suffered very little damage, with only two occurrences of hole-feeding.

**Genus *Rubus* L.**

***Rubus merianii* (Heer) Kolakovskii**

Collection numbers of the fossil material: DB21-244, DB47-168, DB52-332, ZDI040

***Rubus vrsovicensis* Kvaček et Hurnik**

Collection numbers of the fossil material: DB47-163, DB47-354, DB47-5644

Leaves of *Rubus merianii* were palmatelly compound; individual leaflets are oblong to elliptical, 50 mm wide and up to 120 mm long, with broadly cuneate base and acute apex. Margin is simple serrate. *Rubus vrsovicensis* differs mainly in the asymmetrical shape of the leaflets of its compound leaves (Kvaček and Hurník 2000). Both taxa were hydrophilous and occurred as undergrowth in the coal swamps.

Both taxa suffered only a moderate level of damage, due to hole- and margin-feeders.

**Family Ulmaceae**

**Genus *Ulmus* L.**

***Ulmus pyramidalis* Göppert**

Collection numbers of the fossil material: DB30-6804, DB30-6808, DB57-314, DB1-15b DB3-263c, DB5-134, DB5-137, DB5-310, DB5-6807, DB32-6809, DB33-6805, DB36-207d, DB36-214, DB36-6801, DB36-6802, DB36-6803, DB48-6806, DB71-6800, DBJu-539, G-3285, G-4529, G-4538

***Ulmus* sp.**

Collection numbers of the fossil material: DB32-279f, DB5-6904, G-4536, G-4561, G-9017

Leaves of the former species are oblong to ovate, 50–120 mm long, asymmetrical, with rounded to slightly cordate base and attenuate to acute apex. Margin is double to partly triply dentate (Teodoridis, 2001). *Ulmus pyramidalis* was a typical deciduous tree of floodplain forest, like its closest living relatives in North America, such as *Ulmus alata* Michaux (Bůžek, 1971).

Both taxa suffered relatively little damage due mainly to hole- and margin-feeders. Altogether, five distinct FFGs are represented, including mining.

**Genus *Zelkova* Spach**

***Zelkova zelkovifolia* (Unger) Bůžek et Kotlaba**

Collection numbers of the fossil material: DB32-6982, DB33-265b, DB36-6978, DB36-981, DB41-6977, DB41-6980, DB61-6979, DB61-7023, DB61-7024, DB61-7025

Leaves are oval, 50–80 mm long, distinctly coarsely dentate on margin. *Zelkova zelkovifolia* was a deciduous woody species growing in slightly moist habitats. The nearest living relatives are relic plants in Crete (*Zelkova abelicea* (Lamarc) Boisser) and Sicily (*Zelkova sicula* Di Pasquale, Garfí et Quézel), which are densely branched deciduous trees and shrubs (Bůžek, 1971; Kovar-Eder et al., 2004).

This fairly abundant species suffered relatively little damage, caused by three FFGs. Hole-feeding and margin-feeding are the most frequent.

**Order Malvales**

**Family Tiliaceae**

**Genus *Dombeyopsis* Unger**

***Dombeyopsis lobata* Unger**

Collection numbers of the fossil material: DB30-5763, DB5-5764, DB1-258b, DB1-309

Leaves are usually trilobate, with deeply cordate base and entire to slightly dentate margin, quite large, up to 300–400 mm in diameter. Based on its occurrence in coal sediments, it can be concluded, that extinct *Dombeyopsis lobata* was a tree occurring in mires. It was definitely less dependent on high temperature than its descendants are today, since it was accompanied by many deciduous trees. Its closest living relative, *Craigia* W.W. Smith et W.E. Evans, is a relic survivor because only two representatives currently grow at a few locations in southern China and northern Vietnam (Kvaček, 1993).

It suffered little damage with only a few occurrences of hole-feeding and skeletonization recorded.

**Genus *Tilia* L.**

***Tilia brabenecii* Kvaček et Bůžek**

Collection numbers of the fossil material: DB4-6778, DB36-156, DB36-6779, DB36-6787

Leaves are ovate, partly asymmetrical, 50–70 mm in diameter, with simple serrate margins, obtuse apex and strong midrib (Teodoridis, 2001). Lime trees grew in dry habitats located far from the sedimentary environment of the swamp basin. Consequently, in most cases, the fossil leaves were transported by the water. Its closest living relatives occur in the Caucasus and East Asia (China) (Bůžek and Kvaček, 1994).

The few specimens of this species suffered a relatively high level of damage (44.4 %), due to hole-feeding and galling.

**Order Sapindales**

**Family Anacardiaceae**

**Genus *Rhus* L.**

***Rhus noeggerathii* C.O. Weber**

Collection number of the fossil material: DB1-356

This record is for an isolated ovate leaflet, 80 mm long and 37 mm wide, with an obtuse base, acute apex and serrate margin. This species was probably a deciduous shrub or tree, as the living species of the genus *Rhus* currently occur in mesophytic forests (Kvaček et al., 2004).

*Rhus noeggerathii* is represented by one damaged specimen.

**Family Sapindaceae**

**Sapindaceae gen. et sp. indet.**

Collection numbers of the fossil material: DB1-175, DB3-6679, DB36-186, DB41-322, ZDI0029

This morphologically heterogeneous group comprises only a few leaves, one third of which are damaged. The most remarkable finding is the presence of a nepticulid mine in specimen DB36-186.

**Genus *Acer* L.**

***Acer angustilobum* Heer (=*A. dasycarpoides* Heer)**

Collection numbers of the fossil material: DB32-295, DB5-377, DB5-5002, DB5-5003, DB32-5001, DB39-297a, DB57-378, DB57-5004, DB57-5005, DB61-5000

***Acer integerrimum* (Viviani) Massalongo**

Collection numbers of the fossil material: DB5-337, DB5-376, DB5-5044, DB24-192, DB24-5045

***Acer* sp.**

Collection numbers of the fossil material: ZDI0032, G-5483

***Acer tricuspidatum* Bronn**

Collection numbers of the fossil material: DB30-373, DB1-121, DB1-372, DB2-108, DB5-131a, DB5-131b, DB5-131c, DB5-139, DB5-5063, DB5-5064, DB5-5069, DB5-5070, DB5-5072, DB5-5114, DB21-252, DB24-201, DB24-5066, DB24-5067, DB24-5068, ZDI048, DB32-5062, DB32-5071, DB32-5073, DB36-5065, ZDI050, DB72-87, G-2260, G-2264, G-5435, G-5485, G-8072, G-8077, G-8082

Leaves of these taxa are palmate, trilobed to pentalobed with a distinct cordate to broadly cuneate base and differ mainly in the morphology of their lobes. *Acer angustilobum* has leaves up to 120 mm in size with narrow lobes; the leaves of *Acer tricuspidatum* have broader, sometimes quite short lobes and a broader lamina, up to 150 mm long, the leaves of *A. integerrimum* are entire-margined, 40-120 mm in size, with acuminate lobes. All these maples were deciduous trees and characteristic elements in riparian and swamp forests. Their nearest living relatives occur in East Asia and North America, e.g., *A. ginnala* Maximowicz (*A. angustilobum*) and *A. rubrum* L. (*A. angustilobum*). *Acer integerrimum* grew on elevated moist offshore slopes. Related species, like *A. cappadocicum* Gleditsch, occur in the Caucasus and East Asian mesophytic forests (Walther, 1972, Procházka and Bůžek, 1975).

All these species suffered relatively moderate levels of damage by representatives of all the commonest FFGs. However, damage due to piercing, sucking and oviposition was not recorded.

**Genus *Sapindus* L..**

***Sapindus falcifolius* (A. Braun) A. Braun**

Collection numbers of the fossil material: DB36-6690, DB36-6698, DB41-289, DB57-336

Leaflets are oblong to lanceolate, falcate with entire margin and acute apex, usually 20 mm wide and up to 60–80 mm long, probably chartaceous (Bůžek, 1971; Teodoridis, 2001). *Sapindus falcifolius* was a small deciduous tree that grew on the drier slopes. Today genus *Sapindus* includes both deciduous and evergreen species and its members are native in warm temperate to tropical regions of the world.

This taxon suffered very little damage due to hole- and margin-feeders and from sketetonization.

**Family Simaroubaceae**

**Genus *Ailanthus* Desfontaines**

***Ailanthus* sp.**

Collection number of the fossil material: DB24-380

Leaflets are asymmetrical at base, oblong, up to 50 mm long, chartaceous. *Ailanthus* represents a typical element of the mixed mesophytic forest (Teodoridis, 2001). Only one leaflet with a feeding hole was recorded.

**Order Cornales**

**Family Cornaceae**

**Genus *Nyssa* L.**

***Nyssa bilinica* (Unger) Kvaček (syn. *N. haidingeri* (Ettingshausen) Kvaček et Bůžek)**

Collection numbers of the fossil material: DB5-145, DB1-125, DB1-130, DB1-257, DB1-6276, ZDI0009, DB2-111a, DB5-142, DB5-144, DB5-172, DB5-181A, DB5-371, DB5-374, DB5-6275, DB5-6277, DB24-194, DB24-199, ZDI0010, G-9249, G-9257

Leaves are ovate to oblong 10–120 mm wide and 50–250 mm with obtuse base, acute apex and usually an entire margin (Kvaček and Bůžek, 1972). Various fossil remains of *Nyssa* trees are very abundant in the clayey sediments of deltaic successions in the coal basin. *Nyssa haidingeri* was a deciduous, hygrophilous tree, characteristic of marshes and swamp forest. Similar habitats and environmental requirements are recorded for closely related species, such as *Nyssa aquatica* L., which occurs in *Taxodium* swamp forest in the southeastern United States. *Nyssa haigingeri* also shares some morphological features with *Nyssa javanica* (Bl.) Wangerin from Southeast Asia.

This abundant species suffered relatively little damage due to four FFGs. Hole-feeding is the most common.

**Order Ericales**

**Family Ebenaceae**

**Genus *Diospyros* L.**

***Diospyros brachysepala* A. Braun**

Collection number of the fossil material: G-7616

Leaves are oval, chartaceous, with an entire margin, 30–50 mm wide and 40–80 mm long. This species probably did not grow in the swamps and marshes, since its fossil leaves are found predominantly in clayey and sandy-clayey sediments (Sakala, 2000).

One of five specimens is damaged as a result of margin-feeding.

**Family Theaceae**

**Theaceae gen. et.sp. indet.**

Collection numbers of the fossil material: ZDI060, DB24-191, DB32-280, DB32-6769, DB39-6768, DB47-6767, DB73-350, G-8086, G-8090, G-8092, G-8096

Specimens of this heterogeneous, moderately abundant group suffered a relatively high incidence of damage, almost equally due to margin- and hole-feeding.

**Genus *Ternstroemites* Berry, 1916**

***Ternstroemites* sp.**

Collection numbers of the fossil material: DB24-361, DB39-363, DB1-6918, DB2-110, DB2-179, DB5-362, ZDI058, DB36-365, DB36-6915, DB39-6916, DB47-169, DB47-6917, DB47-6938, ZDI041, DB71-6758, DB76-160

Leaves are oval to obovate, with irregularly serrate margins, 60–80 mm long, coriaceous (Bůžek, 1971; Kvaček and Walther, 1984; Kvaček et al. 2004). Representatives of this species were probably low evergreen trees or shrubs, growing on drier slopes, as do their nearest living relatives. They are a distinct themophilic element, which indicates at least subtropical climatic conditions.

This abundant species shows an average level of damage, caused by five different FFGs. Margin-feeding is the most frequent, followed by skeletonization.

**Order Lamiales**

**Family Oleaceae**

**Genus *Fraxinus* L.**

***Fraxinus bilinica* (Unger) Kvaček et Hurník**

Collection numbers of the fossil material: ZDI0004, ZDI0003, ZDI0020, ZDI0023, DB1-15c, DB1-118, DB1-159A, DB1-159B, ZDI0009, DB5-140, DB5-143, DB5-5873, DB32-5872, DB39-5874, DB73-92, G-7648, G-9284, G-9288, G-9289, G-9300, ZDI045

Leaflets are elliptical or ovate, 50–95 mm long and 25–40 mm broad, with an acute apex, round base and regularly serrate margins (Teodoridis, 2001). This deciduous tree was a typical element of floodplain forests. Closely related species currently occur in the same type of habitat in the Atlantic part of North America (for instance *F. pennsylvanica* Marschall) and eastern Eurasia (Knobloch and Kvaček, 1976, Kvaček and Hurník, 2000).

There are 75 moderately damaged specimens of this abundant species, which exhibit the presence of five distinct FFGs. Some of the types of damage are attributable to particular arthropods. Especially, galling, which was studied previously by Knor et al. (2013). An interesting finding is the damage caused by the piercing–sucking of armoured scale insects (Sternorrhyncha: Coccoidea) present on specimen DB1-159 (Plate II. 17, 18).

**Incertae sedis**

***Dicotylophyllum* sp. div.**

Collection numbers of the fossil material: DB39-297b, DB74-147, DB74-148, DB76-5740, G-7615, G-7618

Ovate to elliptical leaves of variable size that have entire to slightly serrate margins and attenuate apices. Fossil remains of these taxa come from different environments throughout the basin.

The most common FFG is hole-feeding, followed by galling and skeletonization.

***Diversiphyllum aesculapi* (Heer) Bůžek**

Collection numbers of the fossil material: DB36-5754, DB36-5755

Leaves are deeply palmate tri-lobed, ca 50 mm in size, chartaceous, with obtuse to slightly cordate bases and entire margins (Bůžek, 1971; Kvaček et al., 2004). This enigmatic plant was probably a climbing liana, with a taxonomic affinity to the family Convolvulaceae.

This less abundant species suffered a low level of damage inflicted by only two FFG (hole-feeding and galling).

***"Ficus" atlantica* Unger**

Collection number of the fossil material: G-3940

***Laria rueminiana* (Heer) G. Worobiec et Kvaček (syn. *"Ficus" truncata* Heer)**

Collection numbers of the fossil material: DB3-34, DB5-32, DB32-5819, DB36-45, DB36-5823, DB36-5824, DB39-5820, DB39-5821, DB41-290, DB41-331, DB72-307, DB72-5822, G-4551

Leaves are ovate, up to 85 mm in diameter with acute apices, broadly cuneate bases and entire margins. Basal venation is actinodromous with strong primary veins (Teodorisis, 2001; Worobiec et al. 2010). More abundant *Laria rueminiana* is known exclusively from the deltaic sand-clayey deposits. Thus, it definitely did not grow in the coal-forming swamps and marshes.

*Laria rueminiana* suffered fairly moderate damage inflicted by three distinct FFGs. Hole-feeding is the most abundant, followed by margin-feeding. Galling was recorded only once.

***Phyllites kvacekii* Bůžek**

Collection numbers of the fossil material: DB36-233, DB57-6458

Leaves (or leaflets) are ovate, short petiolate, small, up to 40 mm in size, with distinct steep secondary veins, which reach a few the coarse teeth on the margin. This fossil species belongs probably to some semideciduous shrubs, but the affinity remains dubious.

***Phyllites nemejcii* Bůžek**

Collection number of the fossil material: DB5-6463

This small leaf is ovate, 45 mm long, with rounded asymmetrical base (Bůžek, 1971). The species was probably a semi-deciduous shrub. Their fossil remains are often found in sandy clayey sediments of deltaic environments. However, their taxonomic relationships remain unclear.

Only one leaf of *Phyllites nemejcii* was damaged. *Phyllites kvacekii* was a more abundant species and suffered relatively little damage inflicted by only by two FFGs, margin-feeding and galling, for both of which there is only a single record.

***Pungiphyllum cruciatum* (A. Braun) Frankenhäuser et Wilde**

Collection numbers of the fossil material: DB27-335, DB36-6535

It was probably a xerophilous element, which did not grow in the coal–forming basin (Kvaček and Walther, 1981). Only two distinct FFGs were recorded for this plant, margin-feeding and mining.

**Dicots - gen. et sp. indet.**

Collection numbers of the fossil material: DB2-7030, ZDI0016, DB21-251, DB24-202a, DB36-226b, DB36-227, DB36-228d, DB5-182, ZDI047, DB73-96, DB4-256, ZDI0005, ZDI0033, ZDI0030, ZDI0024, ZDI0008, ZDI0027, G-4556, G-4568, G-4575a, G-4575b, G-9313, G-9314, G-9334

This heterogeneous group of dicotyledonous plants were relatively abundant and suffered fairly high levels of damage inflicted by five different FFGs. Margin-feeding together with hole-feeding were the most frequent, followed by four records of galling. Skeletonization and mining were both recorded only once.

## 6. Evaluation of results and discussion

### *6.1. Quantitative analysis*

The proportional occurrences of the different FFGs in the whole assemblage correspond closely to those recorded for most taxa with at least 25 specimens (Tab. 5, Fig. 3). The most damaged leaves were attacked by herbivorous arthropods, which cause non-specific traits such as signs of chewing. This includes mainly hole- and margin-feeding. It is thought, that deciduous leaves with a thin lamina are more palatable and thus more vulnerable than evergreen leaves. Nevertheless, hole- and margin-feeding seem to be the most abundant FFGs in both of the above mentioned categories, with some exceptions, like *Daphnogene*, in which galling is the most frequent damage. Other than those previously mentioned the FFGs are very unequally distributed among the taxa. Although rare over all, skeletonization is one of the most frequent FFGs recorded for several abundant taxa.

Proportional occurrence of all types of damage also differs in most taxa with at least 25 specimens. Generally, the occurrence of damage per leaf is a better indicator of the level of damage than the percentage of damaged leaves, since one leaf can be affected by more than one DT. For some taxa, these two approaches result in big differences (Fig. 4).

The comparison of the diversity of DTs among the individual taxa with at least 25 specimens provides rather uniform outputs (Tab. 7). There is no substantial difference among them, with the exception of the few taxa with extreme values. We decided to process the number of occurrences using rarefaction, since this, in our opinion, provides a better way of assessing the relevant diversity. Some authors rarefy the number of leaves, which is influenced by the frequency of damaged leaves. Our approach better reflects the real diversity of the damage caused by arthropods, especially the specialized types of damage. Unfortunately, for only ten of the thirty-nine taxa studied were there a sufficient number of

leaves damaged by the five specialist DTs necessary for assessing the level of diversity. Not surprisingly, deciduous trees prevailed (*Alnus*, *Populus*), as they have relatively high levels of diversity of damage, sometimes reaching the maximum value. In the ranking of all DTs, there are similar situations, with thin leaved trees (*Alnus*, *Fraxinus*, *Nyssa*, *Populus*) having the highest diversity of damage. However, relatively high diversities of damage were recorded for the evergreen tree *Quercus rhenana* and some members of the family Lauraceae. Among the taxa that also suffered intermediate levels of diversity of different types of damage, are both evergreen and deciduous taxa.

Comparing how the diversity of DTs depends on DT frequency confirms a slight increase in tendency (Fig. 5), although this correlation appears to be very weak. Corresponding results are also recorded for the different types of galling damage (Knor et al., 2013).

The localities at Bílina and Břešťany have apparently high overall diversities of different groups of damage types and host plants. The diversity of plant taxa, especially, is much higher than that recorded for Eocene localities on Spitzbergen (Wappler and Denk, 2011), which were chosen for this comparison (see Tab. 8). Although, these localities clearly differ in age and latitude from ours, they offer comparable values for corresponding categories. The results confirmed the presumption of a positive correlation between plant taxa and the general diversity of DTs (Wilf, 2008). This applies to a much lesser extent in the case of less abundant FFGs, like galling and mining.

The differences among individual host plant taxa in the assemblage are very difficult to evaluate, since more distinct environmental and autoecological factors are involved. Even taxonomically very close taxa (e.g., *Populus* ssp.) suffered very different levels of damage. There is also no clear boundary line between evergreen and deciduous species. Susceptibility of plants to insect herbivore activity depends on their local habitat, physiological traits, soil quality, available nutrients, climatic conditions and many others aspects (Fernandes and Price, 1991; Cuevas-Reyes et al., 2003). Due to the fact, that all the specimens collected represent a mixture of plants from different local niches and that each fossiliferous

layer represents a certain time span, the level of damage suffered apparently reflects all the above-mentioned factors.

*6.2. Specific interactions selected*

Most of the DTs cannot be directly attributed to any known organism even at a high taxonomic level. Nevertheless, a few are sufficiently specific for a more accurate taxonomic determination.

The most remarkable finding was undoubtedly the impression of a trichopteran case (Plate I. 3). Although we did not find any fossil caddisflies with this structure, some details strongly confirm this supposition. First of all, the *Taxodium* needles are arranged in such a manner that the likelihood that this could be a random event is extremely improbable. The overlapping of the needles according to the direction of water flow implies that a stream was the most probable environment.

Diverse forms of fossil caddisfly cases (Trichoptera) are known from many fossiliferous sites all over the world (e.g., Jarzembowski, 1995; Leggitt and Cushman, 2001; Leggitt and Loewen, 2002; Heads, 2006**;** Gallego et al. 2011). Trichopteran larvae have been common elements in fluviatile or lacustrine environments since the early Mesozoic. Nevertheless, this is the first record of a caddisfly case built exclusively of *Taxodium* needles. Due to the absence of sclerites or other associated identifiable body parts of individual larvae, it is impossible to determine their taxonomic status. Alternatively, some immature stage (caterpillar) of the family Psychidae (Lepidoptera) could be another possible, but less probable builder of these enigmatic shelters. Nevertheless, the sedimentary environment together with the relatively large amount of the fossil imprints testifies rather to the trichopteran indusia as the most plausible explanation.

Oviposition on the leaf of *Salix haidingeri* (DB21-250) is the second unique finding (Plate I. 15, 16). An incompletely preserved leaf, lacking an apex, 68.14 mm long and 17.12 mm wide, has on its surface dozens of moderately deep, oval impressions, 0.7–0.75 mm in length. Most of them are situated mainly

along both sides of the midrib and orientated parallel to the longitudinal axis. A few of them are randomly situated on the leaf blade and even oriented at right angles to the leaf. According to their size, position and morphology, oviposition by damselflies is the most likely cause of these impressions.

There are a lot of studies on odonatan oviposition in the literature. The various types recorded from the European Upper Cretaceous, Paleogene and Neogene are described by Hellmund and Hellmund (1991, 1996, 1998 and 2002). Similar, although slightly different types of oviposition are also described from the Eocene in Patagonia and attributed to the ichnogenus *Paleoovoidus* (Sarzetti et al, 2009). Fairly diverse arrays of Odonata together with their supposed ovipositions are reported from the upper Oligocene sediments at Rott in Germany (Petrulevičius et al., 2011).

An exact taxonomical determination of the current finding is unclear because of the lack of associated remains of fossil insects. Nevertheless, because of certain morphological traits, members of the family Lestidae are suspected.

The Nepticulid mine in a leaf of Sapindaceae gen. et sp. indet. (DB36-186) is another example of a taxonomically identifiable type of damage (Plate I. 12). Leaf, 52 mm long and 28.8 mm wide, has an ca 68.7 mm long mine of serpentine shape. This mine is in the middle of the basal half of the blade, between the midrib and the right margin and continues by crossing the midrib to the opposite side and finally turns backwards along the left margin. This mine contains pellets of frass, especially in the latter mined parts. Fossil mines are frequently described from different localities, sometimes indicating a long evolutionary occurrence of this kind of plant–insect interaction (Opler, 1973, 1982; Krassilov, 2008).

A spectacular infestation of a leaf of *Fraxinus bilinica* DB1-159 is the last example of a highly specific type of interaction (Plate II. 17, 18). The leaflet is preserved without its apex and is 53.3 mm long and 36.1 mm broad, with an excellently preserved petiolule attached to the rhachis. There are relatively large, circular shaped structures, 5.4 mm in diameter, in the distal right quadrant of the blade of the leaflet. The elevated torus on the outside margin of each structure is approximately 0.8 mm wide and several concentric slightly darker circular lines mark its bottom. Morphologically similar structures

are described from the Middle Eocene of the Messel and Eckfeld maars in Germany and they are considered to be the fossil remains of members of the superfamily Coccoidea (Hemiptera: Sternorrhyncha) (Wappler and Ben-Dov, 2008). However, these infestations are of many individuals, which cover the whole leaf blade, unlike the solitary occurrence on the Bílina specimen.

The presence of fungi is another interesting aspect. Some of the specimens of foliage show signs of decay, including sporocarps. This is the case for specimen DB71-158, which is affected by several dark circular dense corpuscles with a central canaliculus about 0.8–1 mm in diameter (Plate II. 19, 20). The surface of this specimen seems to be also infected with smaller but far more abundant dark dot-like entities. The leaf blade lacks most of its parenchyma, indicating an advanced state of decay. Apothecia of Pyrenomycetes, about 0.5–0.6 mm in diameter, irregularly located in relatively dense formations on the surface of fossilized bark, are present on three specimens (DB23-394, DB25-355 and DB39-393) (Plate II. 21–23). This is evidence that this taphocenosis consisted of a mixture of plant leaves, branchlets, stems and bark of different degrees of decomposition. Although the sediments are of lacustrine and fluviatile origin, some of the specimens must have been on dry land for a relatively long time, during which there was microbial and fungal degradation of the material.

It should be pointed out, that fungi occurred on the surface of the leaves studied relatively often and in many cases the associated damage has striking similarities with arthropod-caused damage. Therefore, differential diagnoses needs to be made in order to avoid misinterpretation of observed interactions. The most important traits of fungal infections are the broad dark rim, created by concentric growths of fungal tissue and necrotic center with a specific texture. This is the especially the case for those fungal infestations that cause damage similar to that of hole feeding insects. Some of these fungal infestations are attributable to known living species, like *Taphrina populina* Fries. Other functional feeding groups, namely those causing damage similar to that resulting from skeletonizing and feeding on the surface, can be confused with decaying processes, which differ mainly in the absence of a reaction rim. The types of damage included in the galling functional feeding group is the most problematic, since the

spectrum of their potential causers is very broad, involving arthropods, nematodes, fungi, bacteria and viruses. Fortunately, the morphology of galls, their size and position together with a strong affinity for specific species of host plant facilitates their efficient and exact specific taxonomic determination (Knor et al., 2013).

## 7. Conclusions

The localities Bílina and Břešťany offer a unique insight into lower Miocene palaeoecosystems in brown coal swamps, marshes and on adjacent higher ground. The extensive collection studied includes nearly 4300 specimens of fossil plant remains. The research focused only on dicotyledonous plants, in order to determine the level of damage caused by arthropods in terms of frequency and diversity.

There are very distinct differences in the incidences of individual functional feeding groups in the whole assemblage. The same is true for individual plant taxa. In both, hole- and margin-feeding are the most frequent, followed by galling. In terms of the diversity of types of damage there are significant differences among the taxa for which there are at least 25 specimens. Deciduous plant taxa with thin leaves, in general, suffered a higher diversity of types of damage. Providing possible explanations for the different frequencies and diversities in the level of arthropod-caused damage is difficult, since many factors are involved.

Only a few of the traces of damage are attributable to known groups of arthropods. Spectacular non-herbivore interactions are represented by impressions of several caddisfly cases built exclusively of *Taxodium* needles, which have not been previously reported.

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## 9. Literature

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**Figure captions.**

Fig. 1 Geographical position of northwestern Bohemia within Europe; map of the Most Basin with the position of the Bílina mine indicated by an arrow.

Fig. 2. Geological section through the Bílina Mine. 1 - Quaternary; 2 - Lake Clayey Horizon; 3 - Delta Sandy Horizon; 4 - Clay Superseam Horizon; 5 - coal clay; 6 - lignite seam; 7 - clayey coal; 8 - neovulcanite bodies of the Střezov Formation; 9 - Upper Cretaceous; 10 - fossiliferous layers (according to Bůžek et al. (1992), modified).

Fig. 3**.** Proportional occurrences (DT/leaf) of all functional feeding groups for the most abundant taxa (N≥25 specimens).

Fig. 4. Comparison of the proportion of leaves damaged and the proportionality of the occurrence of a particular type of damage per leaf for the most abundant genera (N≥25 specimens). Light grey bars indicate the proportion of leaves damaged, dark grey bars the occurrence of damage per leaf. Error bars show standard deviation for the selected taxa.

Fig. 5. Comparison of proportionality between the damage type frequency and their diversity rarefied to the five occurrences in case of the most abundant genera (N≥25 specimens). Vertical axis - damage type diversity, horizontal axis - damage type frequency. $R^2 = 0.8416$, $p = 3.4632$.

Plate I. Insect plant interactions recorded in the Most Basin flora. (1) Detailed photograph of the initial stadium of a cecidomyid gall larva (Diptera: Cecidomyiidae) on *Taxodium dubium* (Cupressaceae) (DB76-106); (2) Branchlet of *Taxodium dubium* (Cupressaceae) with several cecidomyid galls (DB76-106); (3) Detail of caddisfly case built exclusively of *Taxodium* needles (ZD0151); (4) Hole feeding on *Nyssa haidingeri* (DB1-125); (5) Hole and margin feeding on indeterminate dicotyledonous plants with clearly visible reaction rims (ZDI030); (6) Hole feeding on *Rubus merianii* (ZDI040); (7) Margin feeding on *Quercus rhenana* (ZDI046); (8) Margin feeding on *Wisteria* aff. *falax* outlined by a dark reaction rim (ZDI042); (9) Hole feeding on *Carya* sp. (ZDI063); (10) Skeletonization on Sapindaceae gen. et sp. indet. (DB1-175); (11) Skeletonization of *Ternstroemites* sp. (ZDI041); (12) Nepticulid (Lepidoptera) mine on Sapindaceae gen. et sp. indet. (DB36-186); (13) Skeletonization of a leaf of *Parrotia pristina* (DB36-222); (14) Extensive skeletonization of leaves of *Liquidambar europaea* (DB5-136); (15) Oviposition

(Lestidae: Odonata) on *Salix haidingeri* (DB21-250); (16) Enlarged view of an oviposition impression on leaf of *Salix haidingeri* (DB21-250). Figs 2, 4–15 - scale bar = 10 mm; Fig 3 - scale bar = 5 mm; Fig 16 - scale bar =1 mm; Fig 1 - scale bar = 0.5 mm.

Plate II. Further insect plant interactions recorded in the Most Basin flora. (17) Detailed photograph of the armoured scale insect (Coccoidea: Sternorrhyncha) impression on a leaf of *Fraxinus bilinica* (DB1-159); (18) Leaf of *Fraxinus bilinica* with armoured scale insect impression in upper right quadrant (DB1-159); (19) Enlarged view of sporocarps of indeterminate fungi on the leaf of an unidentified dicotyledonous plant (DB71-158); (20) Dicotyledonous plant leaf with sporocarps (DB71-158); (21) Apothecia of pyrenomycetes fungi on bark I (DB25-355); (22) Apothecia of pyrenomycetes fungi on bark II (DB39-393); (23) Apothecia of pyrenomycetes fungi on bark III (DB23-394). Figs 18, 20–23 - scale bar = 10 mm; Figs 17, 19 - scale bar = 1 mm.


Fig 1

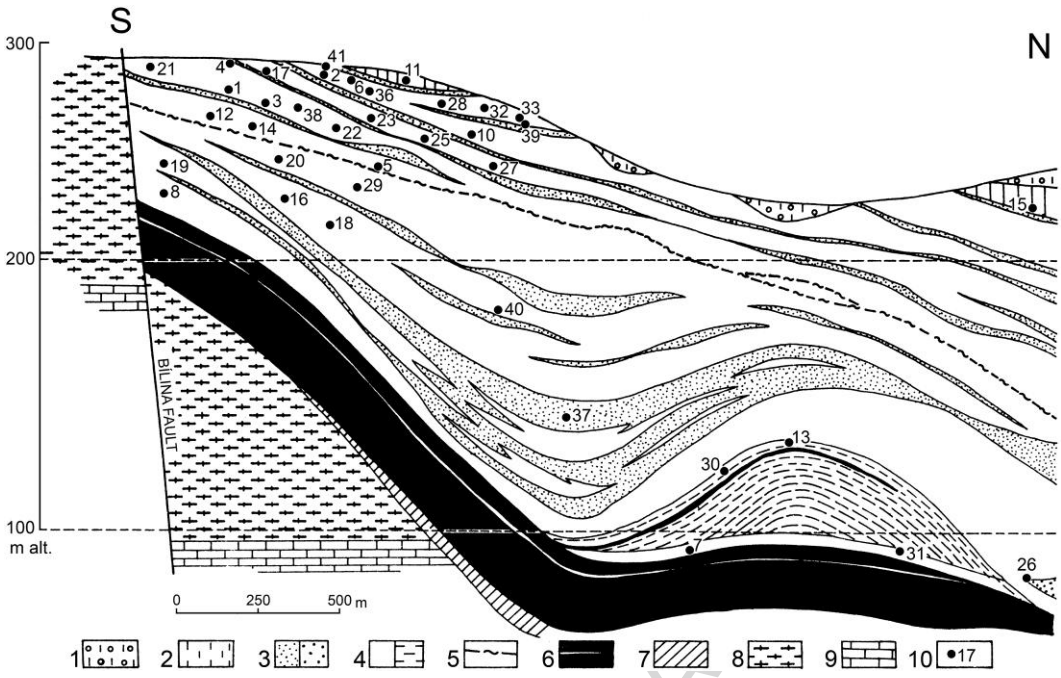


Fig 2

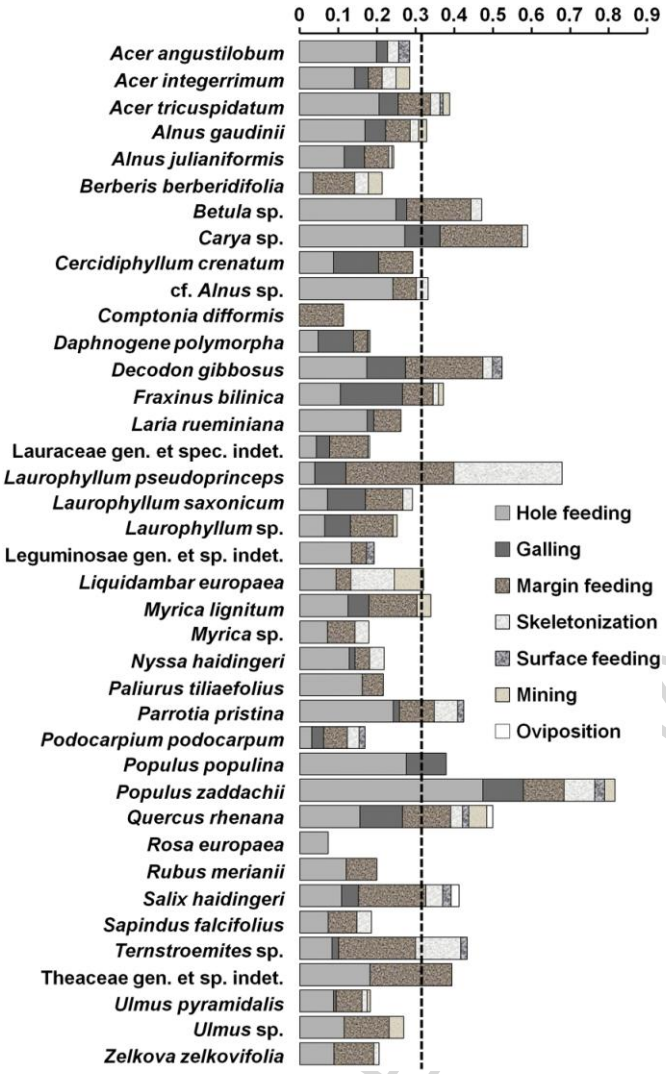


Fig 3

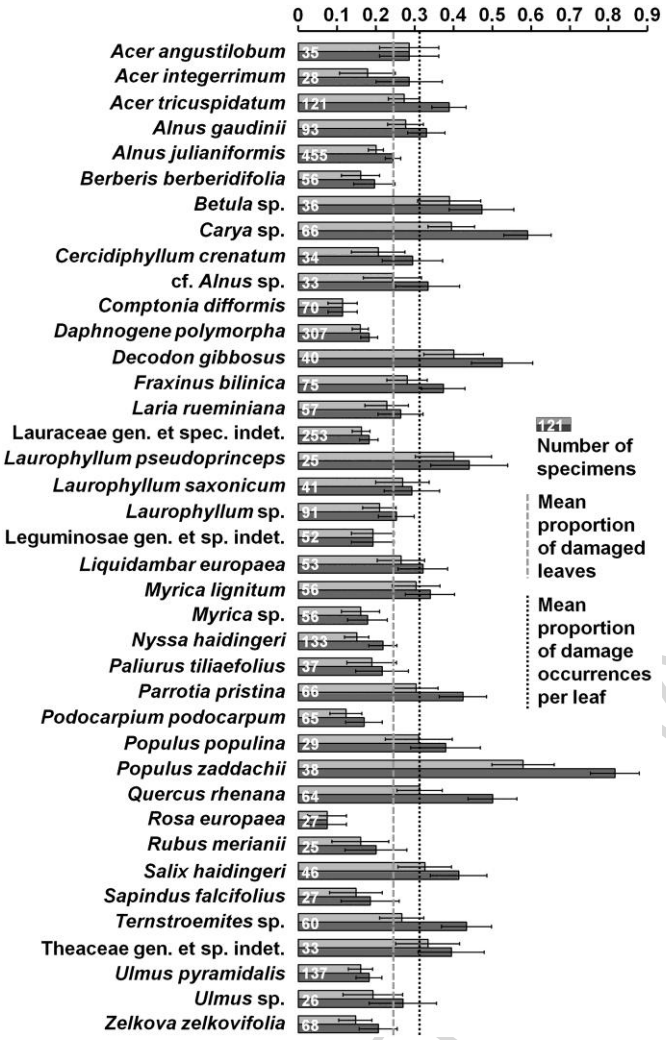


Fig 4

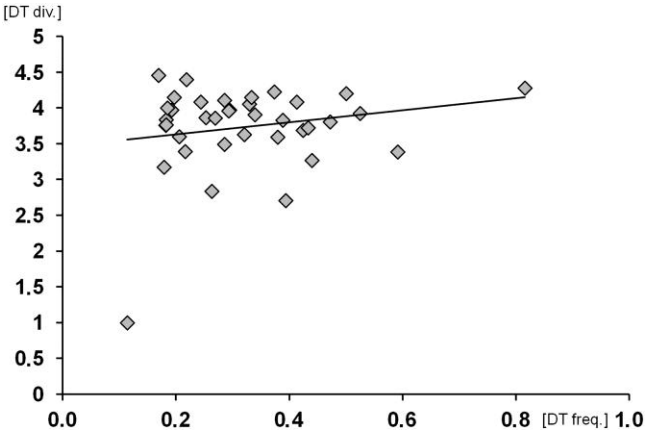


Fig 5

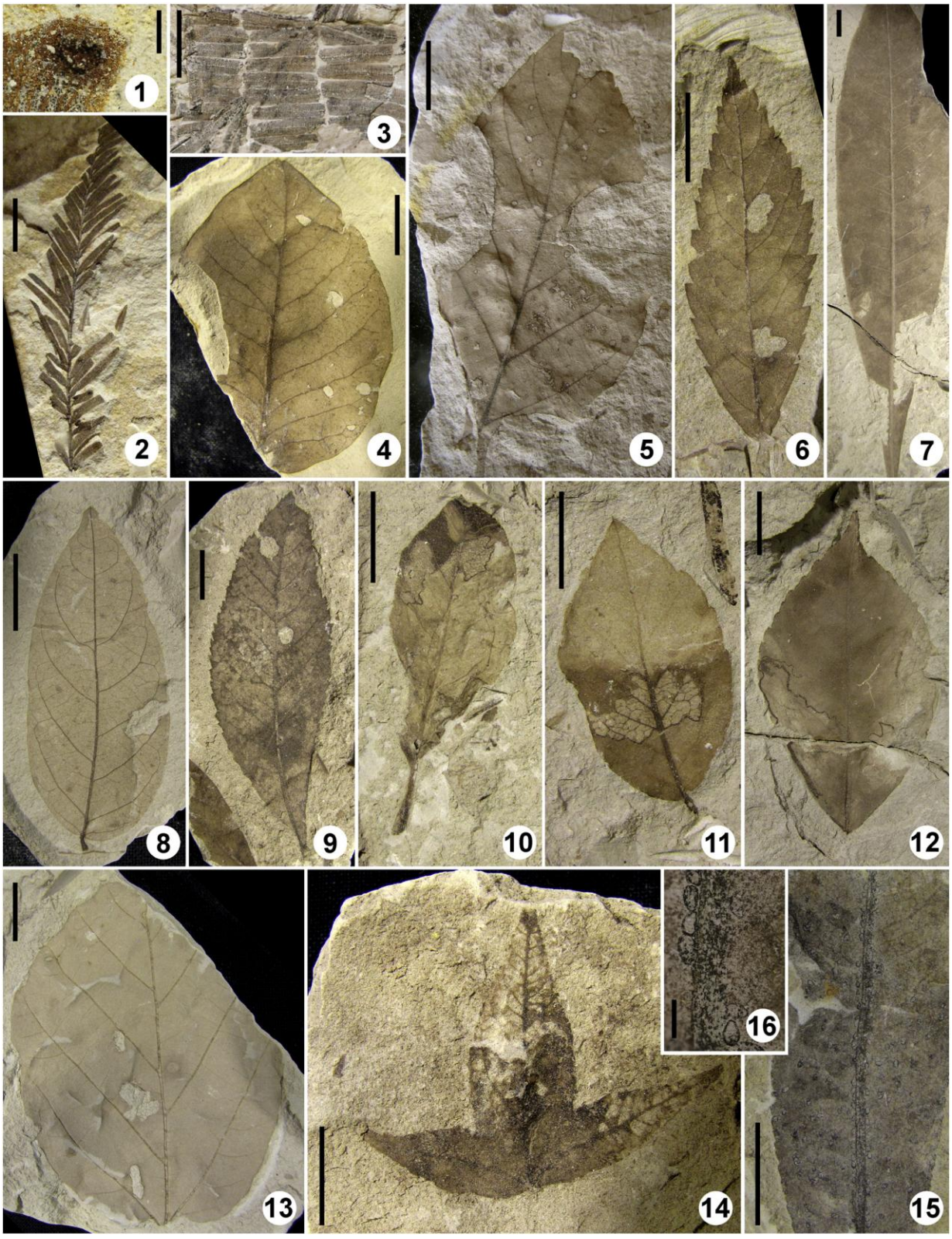


Plate I

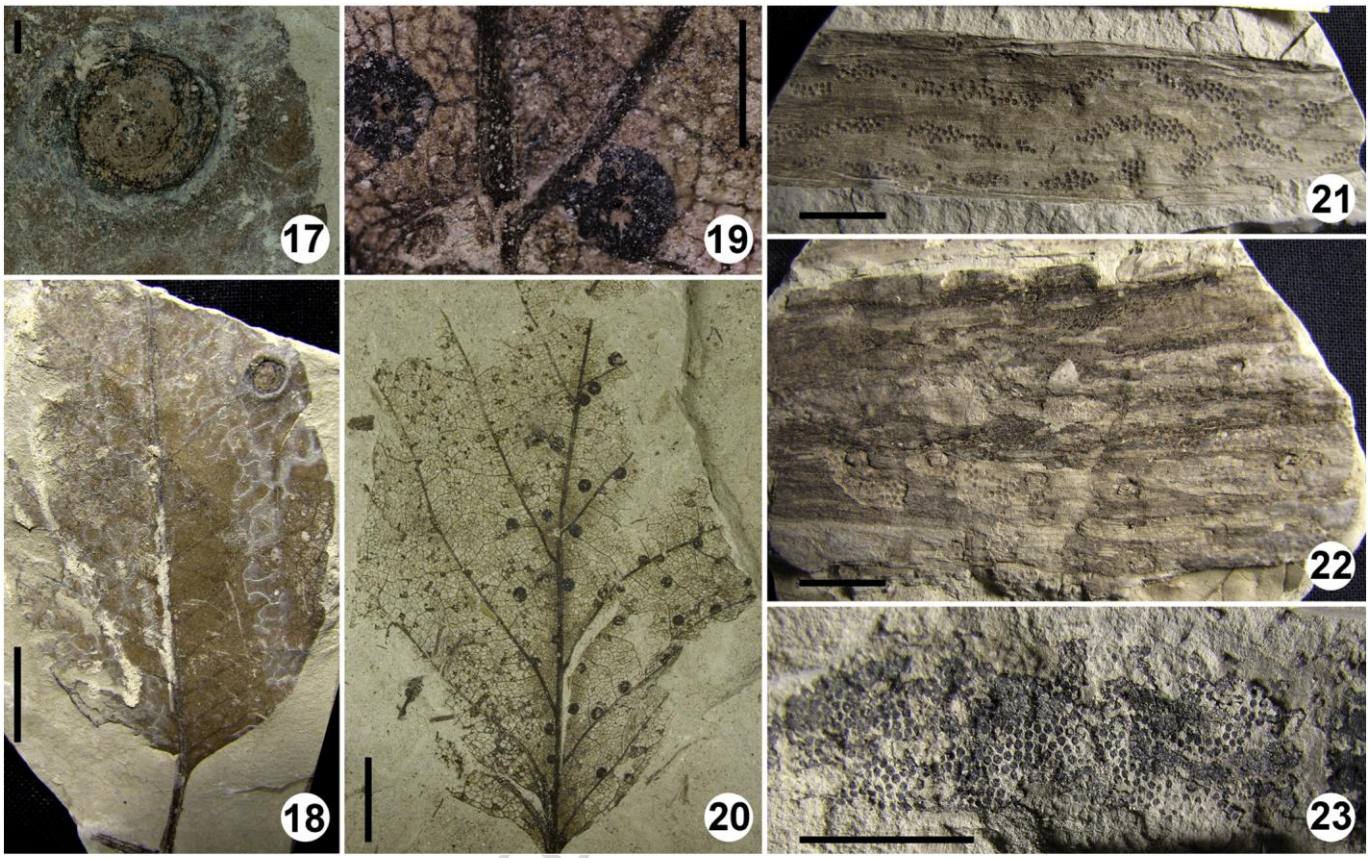


Plate II

**Table 1.** Systematic list of plant taxa (**I**) - individual functional feeding groups, damage type diversity and total number of records of all the different types of damage recorded.

| Taxon | Leaves | Damaged leaves (%) | DT diversity/DT occurrences | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | HF | G | MF | S | SF | M | PS | O | Total |
| **Order Laurales** | | | | | | | | | | | |
| Family Lauraceae | | | | | | | | | | | |
| Lauraceae gen. et sp. indet. | 253 | 16.20 | 5/11 | 3/9 | 4/25 | 1/1 | - | - | - | - | 13/46 |
| *Daphnogene polymorpha* | 307 | 15.96 | 6/15 | 4/28 | 3/11 | 1/1 | - | 1/1 | - | - | 15/56 |
| *Daphnogene* sp. | 7 | 28.57 | 1/2 | - | 1/1 | - | - | - | - | - | 2/3 |
| *Laurophyllum pseudoprinceps* | 25 | 40.00 | 1/1 | 2/2 | 2/7 | 1/1 | - | - | - | - | 6/11 |
| *Laurophyllum saxonicum* | 41 | 26.82 | 2/3 | 3/4 | 1/4 | 1/1 | - | - | - | - | 7/12 |
| *Laurophyllum* sp. | 91 | 20.87 | 3/6 | 4/6 | 2/10 | - | - | 1/1 | - | - | 10/23 |
| **Order Magnoliales** | | | | | | | | | | | |
| Family Magnoliaceae | | | | | | | | | | | |
| *Magnolia kristinae* | 23 | 26.08 | 1/1 | - | 2/5 | - | - | - | - | - | 3/6 |
| *Magnolia* sp. | 1 | - | - | - | - | - | - | - | - | - | - |
| **Order Proteales** | | | | | | | | | | | |
| Family Nelumbonaceae | | | | | | | | | | | |
| *Nelumbium* cf. *buchii* | 2 | - | - | - | - | - | - | - | - | - | - |
| Family Platanaceae | | | | | | | | | | | |
| *Platanus neptuni* | 16 | 37.50 | 2/3 | - | 1/1 | 1/2 | - | - | - | - | 4/6 |
| **Order Piperales** | | | | | | | | | | | |
| Family Aristolochiaceae | | | | | | | | | | | |
| *Aristolochia* sp. | 2 | 50.00 | 2/2 | - | - | - | - | - | - | - | 2/2 |
| **Order Ranunculales** | | | | | | | | | | | |
| Family Berberidaceae | | | | | | | | | | | |
| *Berberis berberidifolia* | 56 | 16.07 | 2/2 | - | 3/6 | 1/2 | - | 1/1 | - | - | 7/11 |
| *Mahonia bilinica* | 1 | - | - | - | - | - | - | - | - | - | - |
| **Order Saxifragales** | | | | | | | | | | | |
| Family Cercidiphyllaceae | | | | | | | | | | | |
| *Cercidiphyllum crenatum* | 34 | 20.58 | 3/3 | 2/4 | 1/3 | - | - | - | - | - | 6/10 |
| Family Hamamelidaceae | | | | | | | | | | | |
| *Liquidambar europaea* | 53 | 26.41 | 2/5 | - | 2/2 | 1/6 | - | 2/4 | - | - | 7/17 |
| *Parrotia pristina* | 66 | 30.30 | 5/16 | 1/1 | 1/6 | 1/4 | 1/1 | - | - | - | 9/28 |
| **Order Vitales** | | | | | | | | | | | |
| Family Vitaceae | | | | | | | | | | | |
| cf. *Ampelopsis* | 7 | 28.57 | 1/2 | - | - | - | - | - | - | - | 1/2 |
| *Vitis stricta* | 11 | 63.63 | 3/5 | - | 2/3 | - | - | - | - | - | 5/8 |
| **Order Myrtales** | | | | | | | | | | | |
| Family Lythraceae | | | | | | | | | | | |
| *Decodon gibbosus* | 40 | 40.00 | 3/7 | 3/4 | 2/8 | 1/1 | 1/1 | - | - | - | 10/21 |
| **Order Fabales** | | | | | | | | | | | |
| Family Fabaceae | | | | | | | | | | | |
| Leguminosae gen. et spec. indet | 52 | 19.23 | 3/7 | - | 2/2 | - | 1/1 | - | - | - | 6/10 |
| *Leguminosites* spec. div. | 10 | 10.00 | - | - | - | - | - | - | 1/1 | - | 1/1 |
| *Podocarpium podocarpum* | 65 | 12.30 | 2/2 | 1/2 | 3/4 | 1/2 | 1/1 | - | - | - | 8/11 |
| *Wistaria* af. *fallax* | 14 | 14.29 | 2/2 | - | - | - | - | - | - | - | 2/2 |

**Table 2.** Systematic list of plant taxa **(II)** - individual functional feeding groups, damage type diversity and total number of the different damage types recorded.

| Taxon | Leaves | Damaged leaves (%) | DT diversity/DT occurrences | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | HF | G | MF | S | SF | M | PS | O | Total |
| **Order Fagales** | | | | | | | | | | | |
| Family Betulaceae | | | | | | | | | | | |
| *Alnus gaudinii* | 94 | 27.66 | 4/16 | 4/5 | 2/6 | 2/2 | - | 2/2 | - | - | 14/31 |
| *Almus julianiformis* | 455 | 20.00 | 8/53 | 5/24 | 5/28 | 1/4 | - | 2/2 | - | - | 21/111 |
| *Alnus menzelii* | 15 | 20.00 | 2/2 | 1/1 | - | - | - | - | - | - | 3/3 |
| *Alnus* sp. | 13 | 7.69 | 1/1 | - | - | - | - | - | - | - | 1/1 |
| cf. *Alnus* sp. | 33 | 24.24 | 5/8 | - | 1/2 | 1/1 | - | - | - | - | 6/10 |
| *Betula* sp. | 36 | 38.89 | 3/9 | 1/1 | 3/6 | 1/1 | - | - | - | - | 8/17 |
| *Carpinus grandis* | 15 | 33.33 | 1/1 | 1/1 | 2/5 | - | - | - | - | - | 4/7 |
| *Carpinus* sp. | 13 | 23.08 | 2/2 | 1/1 | - | - | - | - | - | - | 3/4 |
| Family Fagaceae | | | | | | | | | | | |
| *Quercus rhenana* | 64 | 31.25 | 3/10 | 4/7 | 2/8 | 1/2 | 1/1 | 3/3 | - | 1/1 | 15/32 |
| *Trigonobalanopsis rhamnoides* | 3 | 33.33 | - | 1/1 | 1/1 | - | - | - | - | - | 2/2 |
| Family Juglandaceae | | | | | | | | | | | |
| Juglandaceae gen. et sp. indet. | 3 | 66.67 | 1/2 | - | - | 1/1 | - | - | - | - | 2/3 |
| *Carya serrifolia* | 24 | 54.17 | 3/9 | 1/1 | 1/3 | 1/2 | - | 1/2 | - | - | 7/17 |
| *Carya* sp. | 66 | 39.39 | 2/18 | 5/6 | 2/14 | 1/1 | - | - | - | - | 10/39 |
| *Engelhardia orsbergensis* | 21 | 9.52 | 1/1 | - | 2/3 | - | - | - | - | - | 3/4 |
| *Juglans acuminata* | 23 | 26.07 | 2/2 | 1/1 | 1/3 | 1/1 | - | - | - | - | 5/7 |
| Family Myriaceae | | | | | | | | | | | |
| *Comptonia difformis* | 70 | 11.43 | - | - | 1/8 | - | - | - | - | - | 1/8 |
| *Myrica banksiaefolia* | 6 | 33.33 | - | - | 2/4 | - | - | - | - | - | 2/4 |
| *Myrica integerrima* | 10 | 20.00 | | | 1/2 | | | | | | 1/2 |
| *Myrica lignitum* | 56 | 30.36 | 3/7 | 2/3 | 2/7 | - | - | 2/2 | - | - | 9/19 |
| *Myrica* sp. | 56 | 16.07 | 2/4 | - | 1/4 | 1/2 | - | - | - | - | 4/10 |
| **Order Malpighiales** | | | | | | | | | | | |
| Family Salicaceae | | | | | | | | | | | |
| *Populus populina* | 29 | 31.03 | 4/8 | 2/3 | - | - | - | - | - | - | 6/11 |
| *Populus zaddachii* | 38 | 57.89 | 6/18 | 4/4 | 2/4 | 2/3 | 1/1 | 1/1 | - | - | 16/31 |
| *Salix haidingeri* | 46 | 32.61 | 3/5 | 2/2 | 2/8 | 2/2 | 1/1 | - | - | 1/1 | 11/19 |
| *Salix* sp. | 15 | 26.67 | 2/2 | - | 1/2 | - | - | 1/1 | - | - | 4/5 |
| *Salix varians* | 7 | 14.29 | - | - | - | 1/1 | - | - | - | - | 1/1 |

**Table 3.** Systematic list of plant taxa (**III**) - individual functional feeding groups, damage type diversity and total number of different damage types recorded.

| Taxon | Leaves | Damaged leaves (%) | DT diversity/DT occurrences | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | HF | G | MF | S | SF | M | PS | O | Total |
| **Order Rosales** | | | | | | | | | | | |
| Family Canabaceae | | | | | | | | | | | |
| *Celtis japeti* | 3 | 33.33 | 1/1 | - | 1/1 | - | - | - | - | - | 2/2 |
| Family Rhamnaceae | | | | | | | | | | | |
| *Berchemia multinervis* | 21 | 28.57 | 1/2 | - | 4/5 | 1/1 | - | - | - | - | 6/8 |
| *Paliurus tiliaefolius* | 37 | | 3/6 | - | 1/2 | - | - | - | - | - | 4/8 |
| Family Rosaceae | | | | | | | | | | | |
| Rosaceae gen. et sp. indet. | 5 | - | - | - | - | - | - | - | - | - | - |
| *Crataegus* sp. | 7 | - | - | - | - | - | - | - | - | - | - |
| *Rosa europaea* | 27 | 7.41 | 2/2 | - | - | - | - | - | - | - | 2/2 |
| *Rubus merianii* | 25 | 16.00 | 3/3 | - | 2/2 | - | - | - | - | - | 5/5 |
| *Rubus vrsovicensis* | 3 | 100.00 | 2/3 | - | - | - | - | - | - | - | 2/3 |
| *Sorbus* sp. | 1 | - | - | - | - | - | - | - | - | - | - |
| Family Ulmaceae | | | | | | | | | | | |
| *Ulmus pyramidalis* | 137 | 16.06 | 4/12 | 1/1 | 2/9 | 1/2 | - | 1/1 | - | - | 9/25 |
| *Ulmus* sp. | 26 | 19.23 | 3/3 | - | 1/3 | - | - | 1/1 | - | - | 5/7 |
| *Zelkovia zelkovifolia* | 68 | 14.71 | 3/6 | - | 3/7 | 1/1 | - | - | - | - | 7/14 |
| **Order Malvales** | | | | | | | | | | | |
| Family Tiliaceae | | | | | | | | | | | |
| *Dombeyopsis lobata* | 21 | 19.05 | 2/4 | - | - | 1/3 | - | - | - | - | 3/7 |
| *Tiliia brabenecii* | 9 | 44.44 | 2/4 | 1/1 | - | - | - | - | - | - | 3/5 |
| **Order Sapindales** | | | | | | | | | | | |
| Family Anacardiaceae | | | | | | | | | | | |
| *Rhus noeggerathii* | 1 | 100.00 | 1/1 | - | - | - | - | - | - | - | 1/1 |
| Family Sapindaceae | | | | | | | | | | | |
| Sapindaceae gen. et sp. indet. | 15 | 33.33 | 2/2 | | 1/1 | 1/2 | | 1/1 | | | 5/6 |
| *Acer angustilobum* | 35 | 28.57 | 3/7 | 1/1 | - | 1/1 | 1/1 | - | - | - | 6/10 |
| *Acer integerrimum* | 28 | 17.86 | 2/4 | 1/1 | 1/1 | 1/1 | - | 1/1 | - | - | 6/8 |
| *Acer integrilobum* | 1 | - | - | - | - | - | - | - | - | - | - |
| *Acer* sp. | 12 | 7.69 | 1/1 | 1/1 | - | - | - | - | - | - | 2/2 |
| *Acer tricuspidatum* | 121 | 27.27 | 6/25 | 2/6 | 2/10 | 1/3 | 1/1 | 2/2 | - | - | 14/47 |
| *Sapindus falcifolius* | 27 | 14.81 | 2/2 | - | 1/2 | 1/1 | - | - | - | - | 4/5 |
| Family Simaroubaceae | | | | | | | | | | | |
| *Ailanthus sp.* | 1 | 100.00 | 1/1 | - | - | - | - | - | - | 1/1 | 1/1 |

**Table 4.** Systematic list of plant taxa (**IV**) - individual functional feeding groups, damage type diversity and total number of the different damage types recorded.

| Taxon | Leaves | Damaged leaves (%) | DT diversity/DT occurrences | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | HF | G | MF | S | SF | M | PS | O | Total |
| **Order Santales** | | | | | | | | | | | |
| Family Santalaceae | | | | | | | | | | | |
| *Viscum* sp. | 2 | - | - | - | - | - | - | - | - | - | - |
| **Order Cornales** | | | | | | | | | | | |
| Family Cornaceae | | | | | | | | | | | |
| *Nyssa haidingeri* | 133 | 15.04 | 7/17 | 2/2 | 3/5 | 3/5 | - | - | - | - | 15/29 |
| **Order Ericales** | | | | | | | | | | | |
| Family Ebenaceae | | | | | | | | | | | |
| *Diospyros brachysepala* | 5 | 20.00 | - | - | 1/1 | - | - | - | - | - | 1/1 |
| Family Theaceae | | | | | | | | | | | |
| Theaceae gen. et sp. indet. | 33 | 33.33 | 2/6 | - | 2/7 | - | - | - | - | - | 4/13 |
| *Gordonia* sp. | 2 | - | - | - | - | - | - | - | - | - | - |
| *Ternstroemites* sp. | 60 | 26.67 | 3/5 | 1/1 | 3/12 | 1/7 | 1/1 | - | - | - | 9/26 |
| **Order Lamiales** | | | | | | | | | | | |
| Family Oleaceae | | | | | | | | | | | |
| *Fraxinus bilinica* | 75 | 28.00 | 4/8 | 7/12 | 1/6 | 1/1 | - | 1/1 | - | - | 14/28 |
| *Fraxinus* sp. | 3 | - | - | - | - | - | - | - | - | - | - |
| **Incertae sedis** | | | | | | | | | | | |
| Dicots gen. et sp. indet. | 52 | 46.15 | 7/14 | 2/4 | 3/17 | 1/1 | - | 1/1 | - | - | 14/37 |
| *Dicotylophyllum* sp. div. | 20 | 30.00 | 2/3 | 2/2 | - | 1/1 | - | - | - | - | 5/6 |
| *Diversiphyllum aesculapi* | 16 | 12.50 | 2/2 | 1/2 | - | - | - | - | - | - | 3/4 |
| *"Ficus" atlantica* | 3 | 33.33 | - | 1/1 | - | - | - | - | - | - | 1/1 |
| *Laria rueminiana* | 57 | 22.80 | 3/10 | 1/1 | 1/4 | - | - | - | - | - | 5/15 |
| *Phyllites kvacekii* | 14 | 14.29 | - | 1/1 | 1/1 | - | - | - | - | - | 2/2 |
| *Phyllites nemejcii* | 1 | 100.00 | 1/1 | - | - | - | - | - | - | - | 1/1 |
| *Pungiphyllum cruciatum* | 14 | 14.29 | - | - | 1/1 | - | - | 1/1 | - | - | 2/2 |

**Table 5.** Functional feeding groups - the total number of distinct types of damage/ total number of occurrences of the different types of damage, total number of occurrences and proportional occurrences.

| Leaves | Plant taxa | DT* diversity[1]/ DT occurrences[2] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | HF[3] | G[4] | MF[5] | S[6] | SF[7] | M[8] | PS[9] | O[10] | Total |
| 3509 | 88 | 13/427 | 16/151 | 6/321 | 6/74 | 5/10 | 12/29 | 1/1 | 1/2 | 60/1015 |
| | | DT occurrences per one leaf | | | | | | | | |
| | | 0.1217 | 0.0430 | 0.0915 | 0.0211 | 0.0028 | 0.0083 | 0.0003 | 0.0006 | 0.2893 |

*Damage type; [1]Total number of distinct types of damage [2]Total number of occurrences of the different types of damage; [3]Hole feeding; [4]Galling; [5]Margin feeding; [6]Skeletonization; [7]Surface feeding; [8]Mining; [9]Piercing & sucking; [10]Oviposition

**Table 6.** Number of leaves (in columns) with corresponding number of distinct types of damage and functional feeding groups.

| DT[1]/leaf | FFG[2]/leaf | | | |
|---|---|---|---|---|
| | 0 FFG | 1FFG | 2 FFGs | 3 FFGs |
| 0 DT | 2709 | 0 | 0 | 0 |
| 1 DT | 0 | 615 | 0 | 0 |
| 2 DTs | 0 | 49 | 111 | 0 |
| 3 DTs | 0 | 1 | 10 | 9 |
| 4 DTs | 0 | 0 | 3 | 2 |

[1]Damage type; [2]Functional feeding group

**Table 7.** Individual plant taxa with at least 25 specimens, their damage type diversity, proportional frequency and composition.

| Taxon[1] ≥ 25 specimens | DT/Leaf | Damage Types No. | DT diversity rarefied to the five occurrences | |
|---|---|---|---|---|
| | | | Specialized DTs | Total DTs |
| *Acer angustilobum* | 0.286 | 1, 2, 4, 16, 32[2], 201 | n/a[3] | 3.496 ± 0.823[4] |
| *Acer integerrimum* | 0.286 | 2, 3, 12, 16, 32, 164 | n/a | 4.107 ± 0.673 |
| *Acer tricuspidatum* | 0.388 | 1, 2, 3, 5, 8, 12, 14, 16, 25, 33, 36, 57, 60, 215 | 3.714 ± 0.835 | 3.828 ± 0.834 |
| *Alnus gaudinii* | 0.330 | 1, 2, 3, 12, 14, 16, 20, 33, 41, 57, 85, 90, 145, 153 | 5 ± 1.490 | 4.054 ± 0.798 |
| *Alnus julianiformis* | 0.244 | 1, 2, 3, 4, 5, 7, 8, 11, 12, 13, 14, 15, 16, 32, 33, 34, 36, 57, 105, 110, 143 | 3.473 ± 0.856 | 4.083 ± 0.788 |
| *Berberis berberidifolia* | 0.196 | 2, 3, 12, 13, 14, 16, 39 | n/a | 4.152 ± 0.673 |
| *Betula* sp. | 0.472 | 1, 2, 3, 11, 12, 13, 14, 16 | 0 | 3.808 ± 0.796 |
| *Carya* sp. | 0.591 | 2, 3, 11, 12, 14, 16, 32, 110, 145, 163 | n/a | 3.385 ± 0.848 |
| *Cercidiphyllum crenatum* | 0.294 | 2, 3, 4, 5, 11, 12, 33 | n/a | 3.972 ± 0.675 |
| cf. *Alnus* sp. | 0.333 | 1, 2, 3, 4, 5, 14, 16 | 0 | 4.152 ± 0.673 |
| *Comptonia difformis* | 0.114 | 12 | 0 | 1 ± 0.0 |
| *Daphnogene polymorpha* | 0.182 | 1, 2, 3, 4, 5, 8, 12, 15, 16, 32, 33, 41, 80, 81, 110 | 2.827 ± 0.772 | 3.838 ± 0.796 |
| *Decodon gibbosus* | 0.525 | 2, 4, 5, 12, 14, 16, 31, 33, 49,110 | n/a | 3.923 ± 0.795 |
| *Fraxinus bilinica* | 0.373 | 1, 2, 3, 11, 12, 17, 32, 33, 34, 36, 78, 80, 84, 144 | 3.955 ± 0.756 | 4.226 ± 0.732 |
| *Laria rueminiana* | 0.263 | 2, 3, 5, 12, 32 | n/a | 2.839 ± 0.761 |
| Lauraceae gen. et spec. indet. | 0.182 | 1, 2, 3, 5, 12, 13, 14, 15, 16, 32, 33, 49, 63 | 3.337 ± 0.679 | 3.760 ± 0.868 |
| *Laurophyllum pseudoprinceps* | 0.440 | 2, 12,14, 16, 33, 153 | n/a | 3.271 ± 0.857 |
| *Laurophyllum saxonicum* | 0.293 | 2, 5, 12, 16, 32, 33, 34 | n/a | 3.960 ± 0.737 |
| *Laurophyllum* sp. | 0.253 | 1, 2, 5, 12, 14, 32, 33, 117, 145, 171 | 3.5 ± 0.5 | 3.867 ± 0.822 |
| Leguminosae sp. et gen. indet. | 0.192 | 1, 2, 3, 12, 14, 25 | n/a | 3.972 ± 0.675 |
| Liquidambar europaea | 0.321 | 2, 3, 12, 14, 16, 36, 38 | n/a | 3.629 ± 0.786 |
| *Myrica lignitum* | 0.339 | 2, 3, 8, 11, 12, 14, 34, 41, 89 | n/a | 3.907 ± 0.780 |
| *Myrica* sp. | 0.179 | 2, 12, 17, 50 | n/a | 3.171 ± 0.610 |
| *Nyssa haidingeri* | 0.218 | 1, 2, 3, 4, 5, 9, 11, 12, 14, 15, 16, 21, 24, 34, 78 | 5 ± 0.0 | 4.395 ± 0.673 |
| *Paliurus tiliaefolius* | 0.216 | 1, 2, 3, 12 | 0 | 3.393 ± 0.557 |
| *Parrotia pristina* | 0.424 | 1, 2, 3, 5, 8, 11, 12, 16, 30 | n/a | 3.686 ± 0.803 |
| *Podocarpium podocarpum* | 0.169 | 2, 3, 12, 14, 16, 29, 33, 143 | n/a | 4.454 ± 0.582 |
| *Populus populina* | 0.379 | 2, 3, 5, 12, 15, | n/a | 3.591 ± 0.680 |
| *Populus zaddachii* | 0.816 | 1, 2, 3, 8, 9, 11, 12, 14, 16, 17, 25. 33, 34, 36, 51, 163 | 4.417 ± 0.640 | 4.282 ± 0.740 |
| *Quercus rhenana* | 0.500 | 1, 2, 5, 12, 14, 17, 32, 33, 41, 76, 84, 90, 171, 201, 215 | 4.194 ± 0.677 | 4.200 ± 0.753 |
| *Rosa europaea* | 0.074 | 3, 8 | n/a | n/a[3] |
| *Rubus merianii* | 0.200 | 2, 3, 12, 14, 63 | n/a | 5 ± 0.0 |
| *Salix haidingeri* | 0.413 | 1, 2, 11, 12, 14, 16, 25, 76, 78, 79, 80 | n/a | 4.087 ± 0.788 |
| *Sapindus falcifolius* | 0.185 | 3, 5, 12, 16 | 0 | 4 ± 0.0 |
| *Ternstroemites* sp. | 0.433 | 2, 5, 8, 12, 14, 15, 16, 29, 145 | n/a | 3.723 ± 0.794 |
| Theaceae gen. et sp. indet. | 0.394 | 2, 4,12, 14 | 0 | 2.709 ± 0.653 |
| *Ulmus pyramidalis* | 0.182 | 1, 2, 3, 12, 14, 16, 32, 41, 78 | n/a | 3.767 ± 0.799 |
| *Ulmus* sp. | 0.269 | 2, 3, 5, 12, 41 | n/a | 3.857 ± 0.639 |
| *Zelkova zelkovifolia* | 0.206 | 2, 3, 5, 12, 13, 14, 16 | 0 | 3.597 ± 0.803 |

[1]Taxa in alphabetical order; [2]Specialized damage type; [3]Less than five occurrences; [4]Standard deviation,

**Table 8.** Comparison of plant diversity and diversity of particular types of damage recorded in the lower Miocene deposits at Bílina and Eocene deposits on Spitzbergen[1].

| Locality | Plant diversity rarefied to 400 leaves | Total DT diversity rarefied to 400 leaves | Specialized DT diversity rarefied to 400 leaves | Gall diversity rarefied to 400 leaves | Mine diversity rarefied to 400 leaves |
|---|---|---|---|---|---|
| Bílina | 66.1 ± 2.9 | 24.2 ± 2.7 | 11.8 ± 2.3 | 6.7 ± 1.5 | 2.7 ± 1.3 |
| Renardodden[2] | 25.9 ± 1.0 | 16.8 ± 0.9 | 8.3 ± 0.8 | 5.5 ± 0.6 | 1.9 ± 0.8 |
| Aspelintoppen[2] | 20.8 ± 0.7 | 19.7 ± 1.3 | 10.6 ± 1.0 | 4.5 ± 0.7 | 2.7 ± 0.5 |
| Firkanten[2] | 26.7 ± 1.3 | 21.6 ± 1.6 | 10.3 ± 1.3 | 2.8 ± 0.4 | 3.6 ± 0.6 |

[1]Wappler and Denk, 2011; [2]Localities of three different stratigraphic fossiliferous levels

## Highlights

Arthropod interactions on plant leaves were studied from Miocene horizons.

Diversity and frequency of interactions on various plant taxa were observed.

Specific damage types attributable to known causers were analyzed.

Certain host specific interactions exhibit long evolutionary stasis.